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Sexual dimorphism in postcloacal scales in the northern caiman lizard (*Dracaena guianensis*)

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Morphological differences between males and females are common among reptiles. A particularly interesting sexually dimorphic feature whose function is largely unknown is the number and pattern of specific scales. Several lizard species possess an arrangement of centered scales near the cloacal region that differ between the sexes and can be used for sex determination. The presence of postcloacal buttons, sexually dimorphic postcloacal scales on both sides of the body, is an exclusive trait in the subfamily Tupinambinae and is only poorly documented. Here, we investigate postcloacal scales in northern caiman lizards (*Dracaena guianensis*) housed at the Vienna Zoo. For a period of two years, we documented scale patterns and performed morphometric measurements of individuals of different age classes. Caiman lizards were CT scanned to confirm the sexes. Males exhibit three raised postcloacal scales in a row behind the left and right leg, while females possess one or two large scales surrounded by several smaller scales. The study provides the first evidence that these scales can function as a reliable trait to distinguish the sexes regardless of age or reproductive status. The sexually dimorphic bilateral scale pattern is present immediately after hatching and does not change during development. Scales only increase in thickness and length during growth. We further demonstrate that sexual size dimorphism (SSD) exists in juveniles during ontogenetic development. Juvenile females had a larger SVL, body length, tail length and higher weight compared to juvenile males. This SSD could not be confirmed in adults, and sex determination based on SSD seems unreliable.

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computed tomography, postcloacal buttons, reptile, sexing, Teiidae

Introduction

Sexual dimorphism, the difference in morphology between male and female members of the same species (Andersson 1994), is common in the animal kingdom and particularly in reptiles (Butler and Losos 2002; Olsson et al. 2002). Several studies identified sexual size dimorphism (SSD) in reptiles by comparing morphological traits such as body length (i.e., snout-vent, carapace, or plastron length), as well as head width, head length, body length, and body mass (Olsson et al. 2002; Schwarzkopf, 2005; Cox et al. 2007; López Juri et al. 2018; Yang et al. 2019) between the sexes. Selection for such difference might pose an advantage in intrasexual mate competition (Salvador et al. 1995; Martin and Salvador 1997; Cox et al. 2003; Naretto et al. 2014) or provide a fecundity advantage (Olsson et al. 2002; Cox et al. 2003; López Juri et al. 2018) to store larger energy reserves or more eggs/embryos (Du and Lu 2009).

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The widespread biological phenomenon in which traits of one sex are characteristically larger than those of the opposite sex for a given population or species (Cox et al. 2003) differs greatly among lizard species. For example, male-biased SSD reaches extremes of over 50% longer snout-vent length of males compared to females in anoles (*Anolis* spp.) (Butler et al. 2000), Neotropical ground lizards (*Tropidurus* spp.) (Pinto et al. 2005), marine iguanas (*Amblyrhynchus cristatus*) (Wikelski and Trillmich 1997), and monitor lizards (*Varanus* spp.) (Cox et al. 2007). By contrast, female's snout-vent length (SVL) exceeds that of males by as much as 20% in bush anoles (*Polychrus* spp.) (Cox et al. 2007), common sun skink (*Eutropis multifasciata*) (Shrma 2022), and legless lizards (*Aprasia* spp.) (Cox et al. 2007). Females have longer SVL even in horned lizards (*Phrynosoma* spp.) (Zamudio 1998) and South African dwarf chameleons (*Bradypodion* spp.) (Stuart-Fox 2009).

Several other morphological traits differing among sexes are ornamentations like dewlaps (Nicholson et al. 2007), horns (Amarasinghe et al. 2009; Wikramanayake et al. 2021), femoral pores (Avila-Pires 1995) or hidden characters as the number of vertebrae (Arnold 1973; Kaliontzopoulou et al. 2015). A particularly interesting sexually dimorphic feature whose function is largely unknown is the number and dimension of specific scales. For example, preanal scales and preanal plates, the scales situated in front of the cloaca of four-lined ameiva (*Holcosus quadrilineatus*), are dimorphic traits (Harvey et al. 2012). In males, a large anterior preanal plate projects posteriorly separating two small preanal plates, whereas small granular scales surround a single large preanal plate in females (Harvey et al. 2012). Males of this species also possess two enlarged postanal/postcloacal scales, also called postanal plates, situated immediately posterior to the postanal ridge and separated by 2–4 granular scales (Pietruszka 1981; Harvey et al. 2012). These scales are absent in most South American tegus but are present in western and Central American jungle-runners (*Ameiva* spp.), ameivas (*Holcosus* spp.), whiptail lizards (*Aspidoscelis* spp.), and some species of racerunners (*Cnemidophorus* spp.) (Pietruszka 1981; Ashton 2003; Harvey et al. 2012). Enlarged postanal scales are even present in males of anoles iguanian lizards (*Anolis* spp.) (Malhotra and Thorpe 1997; Lovern et al. 2004), common Indian monitor (*Varanus bengalensis*) (Deraniyagala 1958), spiny lizards (*Sceloporus* spp.) (Ballinger et al. 1996; Mueller and Moore 1969; Weintraub 1969), horned lizards (*Phrynosoma* spp.) (Whiting and Dixon 1996) and side-blotched lizard (*Uta* spp.) (Stejneger 1895; Mayhew and Tinkle 1968). In all the above-mentioned taxa, postanal scales are a dimorphic trait already present in juveniles.

A further scale dimorphism is the presence of a small cluster of 2–3 slightly raised and enlarged rounded scales behind the vent of males, so-called postcloacal buttons. This character is not well documented and was only briefly described in the 16 species of the subfamily Tupinambinae (Fitzgerald et al. 1991; Harvey et al. 2012; Silva et al. 2018; Borczyk and Skawiński 2019). The only available picture of postcloacal buttons was documented in one male of dwarf tegu (*Callopistes maculatus*) (Harvey et al. 2012, fig. 30, p. 35). Limited information is available about the presence of similar scales in the northern caiman lizard: *Dracaena guianensis* Daudin, 1802. Individuals with three enlarged and raised scales in a row behind the vent are considered males. However, sexual scale dimorphism is only known empirically; the precise structure and variation has never been described.

Northern caiman lizards can grow up to a meter long and are among the largest lizards in South America (Vanzolini and Valencia 1965; Avila-Pires 1995). Captive individuals can reach up to 412 mm in snout-vent length (SVL) (Duellman 1978), while males found in the wild ranged from 300–355 mm SVL and are larger than females ranging from 236–278 mm SVL (Mesquita et al. 2006). Similarly, two males housed at Prague Zoo are larger and heavier than one female kept in the same facility (Rehak 1999). However, no SSD in body size and head size correlation were found (Mesquita et al. 2006), even if males appeared to be bigger than females (Rehak 1999; Mesquita et al. 2006; Frýdlová and Frynta 2015).

The Vienna Zoo houses *D. guianensis* since 2007, and some individuals exhibit three scales arranged in a row, while others have one or two larger scales surrounded by several small scales to the right and left of the cloaca (Fig. 1). These potentially sexually dimorphic postcloacal buttons are present instantly after hatching. To investigate this idea, we documented scales of eight juveniles for a period of almost two years starting at the age of two months, and eventually identified the corresponding sex with computed tomography scans. Similarly, we examined postcloacal scales of adult *D. guianensis* housed at the Vienna Zoo and tested SSD by conducting continuous measurements of body weight, SVL, head-, body- and tail length on every individual. As such we determined if individuals can be sexed immediately after hatching and how SSD supports discrimination between the sexes.

Methods

Studyspeciesandlocation

The study was conducted with a captive population of *Dracaena guianensis* at the Vienna Zoo (Vienna, Austria). The population consisted of 15 individuals at the start of this study and currently nine individuals are housed in the Terrarium House in Vienna while six individuals were transferred to other Zoos. Individuals were pair- or single-housed in large terraria (245 × 170 × 190 cm or 100 × 75 × 100 cm), with a water area (respectively 100 × 150 × 20 cm and 100 × 75 × 15 cm). All terrariums were equipped with rocks, big branches, plants, and coco peat as a substrate. Individuals were housed under 12-hour light and 12-hour dark cycles. During the 12-hour light period illumination was provided by a combination of metal-halide lamps as well as heating lamps (250 W)

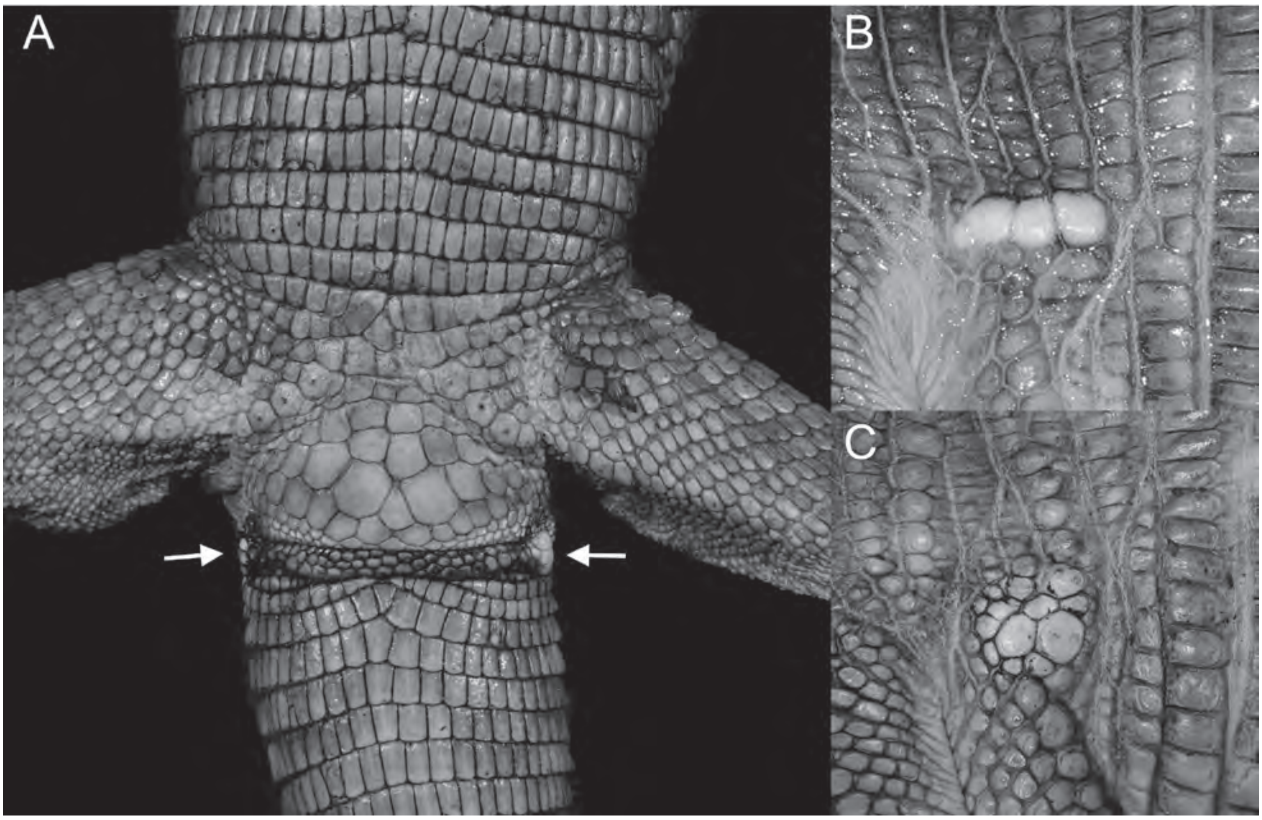

Figure 1. Overview of postcloacal scales of *Dracaena guianensis*. **A.** Arrows show location of sex dimorphic scales left and right of the cloaca; **B.** Three male postcloacal buttons in a row and **C.** One large female scale surrounded by several smaller and one larger scale in a circular pattern.

shining for 6 hours per day and UVB lamps shining for 9 hours per day (150 W for small terrariums, 300W for large terrariums). The air temperature was approximately 30.1 °C (SE ± 0.1; range: 27.8–32.7), the water temperature was 27.9 °C (SE ± 0.1; range: 25.8–33.6) and relative humidity reached 66.3% (SE ± 0.7; range: 47.4–96.3). Individuals were fed three times a week with either snails (*Achatina* spp., *Helyx* spp.) without shells, or freshwater fish fillet (*Salmo trutta* ssp.) dusted with Spirulina powder.

Data collection

Monthly morphometric measurements were taken from October 2018 to September 2020 on a total of 15 individuals of *D. guianensis* of different age classes (Table 1). As no information is available when individuals sexually mature, hence reach adulthood, we determined individuals older than two years as adults according to a single documented incident of a female (ID 923) born in the Vienna Zoo, that laid 6 eggs at the age of 2 years and 4 months at the Basel Zoo. Accordingly, seven individuals were classified as adults at the start of the measurements. Two adult individuals were born in 2005 in Peru and were transferred to the Vienna Zoo in 2007. The remaining five adult individuals were bred and raised at the Vienna Zoo in 2015 and 2016. Eight individuals were juveniles that hatched in October 2018. One week after hatching, the first morphometric measurements were taken. To determine SSD, we took monthly head length, body length, tail length, and weight measurements from October 2018 to July 2020 ($N = 21$) for juvenile individuals and additionally from January to September 2020 ($N = 9$) for adult individuals. Depending on the size of the individuals we used a dial caliper or measuring tape to determine length. The head was measured from the tip of the snout to the posteri-

Table 1. Summary of *Dracaena guianensis* study population and methods used to determine sex. Individual identification number (ID).

ID	**Birth year**	**Age class**	**Sex**	**Sex-determination Method**		
				Scales	**CT scan**	**Reproduction**
930	2018	juvenile	female	x	x	
925	2018	juvenile	male	x	x	
927	2018	juvenile	female	x	x	
928	2018	juvenile	male	x	x	
142	2016	adult	male	x	x	x
370	2016	adult	female	x	x	x
358	2005	adult	female	x	x	x
361	2005	adult	male	x	x	x
366	2015	adult	female	x	x	
368	2016	adult	female	x		
369	2016	adult	male	x		
929	2018	juvenile	female	x		
923	2018	juvenile	female	x		x
924	2018	juvenile	male	x		
926	2018	juvenile	male	x		

or end of the parietal scale, the body length from the posterior end of the parietal scale until the cloaca, and from the cloaca to the tip of the tail was considered as tail length. SVL was calculated as the sum of head length and body length. Postcloacal scales of juveniles were photographed from December 2018, while monthly measurements and photo documentation of scales of all 15 individuals were performed from June 2019 – July 2020 (*N* = 14). We used a dial caliper to measure postcloacal scales length to the nearest 0.01 mm. Depending on the visual appearance of scales we either measured the length of three same-sized scales arranged in a row or the diameter of one large scale on the left body side of the individuals (Fig. 1).

In August 2022 nine *D. guianensis* underwent a health check and were sexed with the help of computed tomography (CT) at the University of Veterinary Medicine, Vienna. Six individuals (2 adults and 4 juveniles) of the study group were transferred to Liberec and Basel Zoo before the CT scans and were not included in the analysis. All examinations were performed in awake animals positioned in a box in sternal recumbency with a dual energy 128-slice helical CT (Siemens Somatom X.cite, Vienna, Austria), using 80–100 mAs, 130 kV, rotation time 1.5 s, pitch 0.8, and slice thickness 0.5 to 0.75 mm. The scans were reformatted with an ultra-sharp bony and a soft tissue kernel, FOV 55 × 55 mm, matrix size 512 × 512, increment 0.6 mm, and then evaluated in a bony and soft tissue window. Image interpretation was done with multiplanar reconstruction with JIVEX, Version 5.3.0.2 RC01 (Visus Health IT GmbH, Bochum, Germany). Contrast-enhanced images were gained using intravenous iodine (Optiray(R) 300 mgJ/ml, Guerbet, France) with a dosage of 2 ml/kg BW.

Statisticalanalysis

To test SSD, we compared morphometric parameters (SVL, head size, body size, tail length, and weight) of either all adults or all juveniles between the sexes using generalized linear mixed models (GLMMs) with normal distribution, identity link function and Student's t statistic for post hoc comparisons. The sex of individuals transferred to other zoos, that could not be confirmed by CT scans or a reproductive event (juvenile: 924,926, 929; adult: 368, 369) was assigned according to the visual appearance of scales. The morphometric parameters were entered as dependent variables, with sex as predictor variables and individual and point of measurement as random variables to correct for repeated measurements of the same individual. Statistical analyses were performed with the program SPSS 26 (IBM SPSS Statistics, USA).

Results

Dracaena guianensis possess distinct postcloacal scales behind their left and right hind legs (Fig. 1A). Male individuals exhibit three same-sized and raised scales in a row (postcloacal buttons) and females have a single large center scale bordered in some cases by a second larger scale and 4–7 not raised smaller scales (Fig. 1B, C). Female scales are arranged in a circular or curved pattern and never form a linear row. The sexual dimorphic scales are similar on both sides of the body and visible immediately after hatching. The form of the scales remains consistent but increases in size with increasing age (Fig. 2). Male buttons length averaged 6.70 mm (range 5.21–8.13; *N* = 3) in adults and ranged from 2.89 to 5.72 mm in juveniles (*N* = 4) during the age of 8–21 month. The single center scale of adult females averaged 3.57 mm (range 2.18–3.47; *N* = 4) and ranged from 1.43 to 2.62 mm in 8–21 month-old juveniles (*N* = 4).

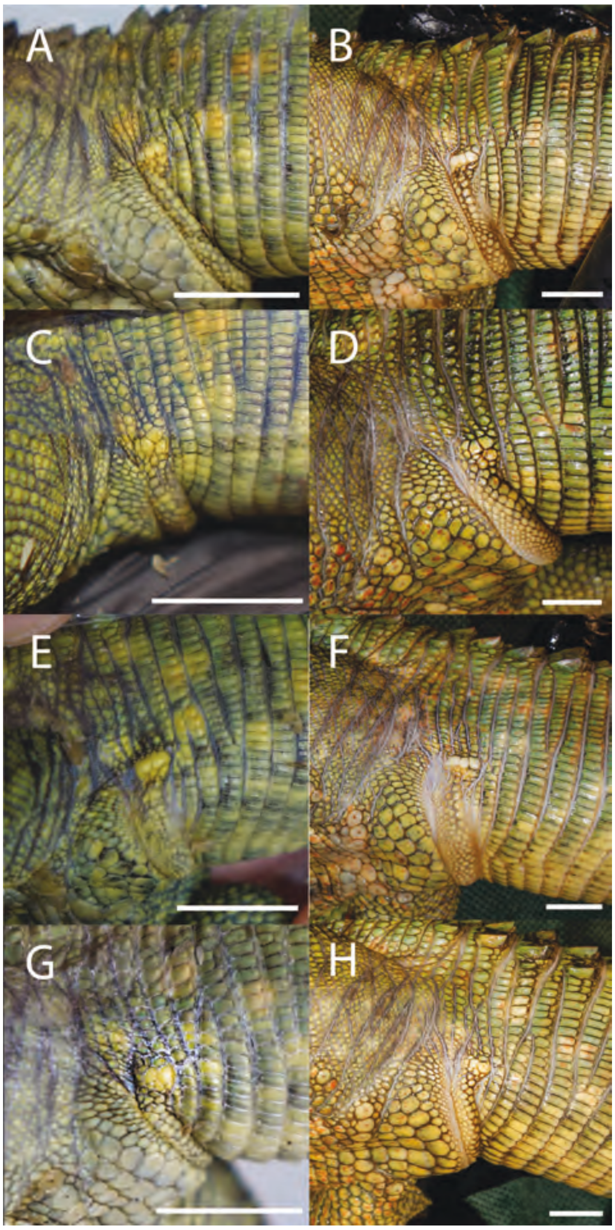

Figure2. Scale comparison between 3 month (left side) and 3 years and 10 month (right side) old *Dracaena guianensis* individuals from the Vienna Zoo. **A, B.** Male ID 925; **C, D.** Female ID 927; **E, F.** Male ID 928; **G, H.** Female ID 930. Pictures taken in January 2019 (age: 3 month) and in August 2022 (age: 3 years and 10 month). Scale bar: 1 cm.

Out of 15 individuals (8 juveniles and 7 adults) included in the current study, the sex of nine individuals (4 juveniles and 5 adults) could be determined by computed tomography scans (Fig. 3). All individuals could be identified by their gonads and scans showed visible testis and active ovary. The resulting sex corresponded to the above-described respective male or female scale pattern. In addition to scale pattern, the sex of one juvenile (ID 923) could be confirmed as female by a reproductive event in which the individual deposited six eggs at Basel Zoo (Table 1). The sex of the remaining five individuals (2 adults and 3 juveniles) that were not CT scanned was exclusively classified according to scale patterns based on the results of this study and included in SSD analysis.

Sexual size differences

Male and female juveniles differed in body length (GLMM: $F_{1,166}$ = 4.992, P = 0.027; Fig. 4A), SVL (GLMM: $F_{1,166}$ = 4.162, P = 0.043; Fig. 4B), tail length (GLMM: $F_{1,166}$ = 6.577, P = 0.011; Fig. 4D), and weight (GLMM: $F_{1,166}$ = 6.025, P = 0.015; Fig. 4E) during the first 21 months after hatching. We found no difference in head length (GLMM: $F_{1,166}$ = 2.183, P = 0.141; Fig. 4C). Female juveniles had a longer SVL (GLMM: pairwise comparison, female vs. male: *ß* = 14.208, SE = 6.964, t = 2.040, P = 0.043), body (GLMM: pairwise comparison, female vs. male: *ß* = 11.310, SE = 5.062, t = 2.234, P = 0.027), tail (GLMM: pairwise comparison, female vs. male: *ß* = 38.583, SE = 15.045, t = 2.565, P = 0.011), and were heavier (GLMM: pairwise comparison, female vs. male: *ß* = 96.845, SE = 39.456, t = 2.455, P = 0.015) compared to male juveniles. Contrary to the juveniles, the adult individuals showed no SSD in SVL, head-, body-, tail-length, or weight (GLMM: $P > 0.05$ for all parameters; Table 2). The above mentioned differences remain consistent when removing individuals whose sex could not be confirmed by CT scans or a reproductive event from the respective SSD analysis (juveniles: 924, 926 and 929, or adults: 368 and 369, Suppl. material 1).

Discussion

The *Dracaena guianensis* population at the Vienna Zoo has sexually dimorphic scales behind their left and right hind legs, at the end of the cloacal opening. Males exhibit three raised postcloacal scales in a row, termed postcloacal buttons, while females possess one or two large scales surrounded by several smaller scales in a circular pattern. The scales to the right and left of the cloaca are already present after hatching (personal observation by the authors) and provide a reliable sexual characteristic that can be used to easily identify the sex of an individual regardless of age or reproductive status. The scale pattern does not change during development, merely the thickness of the buttons and the length of the scales of both males and females are altered during growth. In juveniles, differences in the pattern are visible between the sexes, but buttons and scales are flat and level with surrounding body scales.

Table 2. Body measurements for *Dracaena guianensis* individuals from the Vienna Zoo. Data are estimated means ± standard error (SE) of generalized linear mixed models. 21 measurements were performed for juveniles, nine for adults. Sex was assigned according to subsequent classification (see Table 1); sample sizes in parentheses.

Class	Sex	SVL (mm)	Head length (mm)	Body length (mm)	Tail length (mm)	Weight (g)
Juvenile	Male (4)	196.42±11.11	52.37±2.56	144.05±8.62	340.02±22.23	327.02±49.35
	Female (4)	210.63±11.11	55.27±2.56	155.36±8.62	378.61±22.23	423.87±49.35
Adult	Male (3)	336.61±20.70	83.35±4.32	253.26±16.64	621.33±30.25	1,585.30±295.94
	Female (4)	355.94±17.94	83.35±3.75	272.58±14.42	578.56±26.22	1,910.83±256.43

Scutellations around the anal region play an important role in identifying the sex of several lizard species and occur in various types among the suborder Lacertilia. Preanal and postanal scales are described in both sexes, situated before or after the cloaca, usually in a central position. Such scales were observed in males of several families among the suborder Lacertilia, for example, family Dactyloidae (Malhotra and Thorpe 1997; Lovern et al. 2004), Varanidae (Deraniyagala 1958), Liolaemidae (Fernando et al. 2019), Phrynosomatidae (Mayhew and Tinkle 1968; Ballinger et al. 1996; Whiting and Dixon 1996), Xantusiidae (Davis and Leavitt 2007) and Teiidae (*Ameiva* spp., *Holcosus* spp., *Aspidoscelis* spp., and *Cnemidophorus* spp. (Ashton 2003; Pietruszka 1981; Harvey et al. 2012)), but were reported as not present in its subfamily Tupinambinae (Pietruszka 1981; Ashton 2003; Harvey et al. 2012).

The only visual representation of particular bilateral scales, postcloacal buttons, in Tupinambinae, comes from a male dwarf tegu (*Callopistes maculatus*) (Harvey et al. 2012, fig. 30, p. 35). *Dracaena guianensis* studied in the present work show sex dimorphic scales located laterally on both sides of the body immediately after the cloaca (Fig. 1) corresponding to the few descriptions of postcloacal buttons (Harvey et al. 2012). Although both enlarged postanal plates and postcloacal buttons, indicate the sex in lizards, it is significant that buttons have only been observed in the subfamily Tupinambinae, while enlarged postanal plates were absent in the studied animals. Further studies should investigate the hereby suggested divergent evolution of scales in species of the family Teiidae and take a closer look at postanal/cloacal scales of species among the subfamily Tupinambinae, and the particular interesting congeneric species

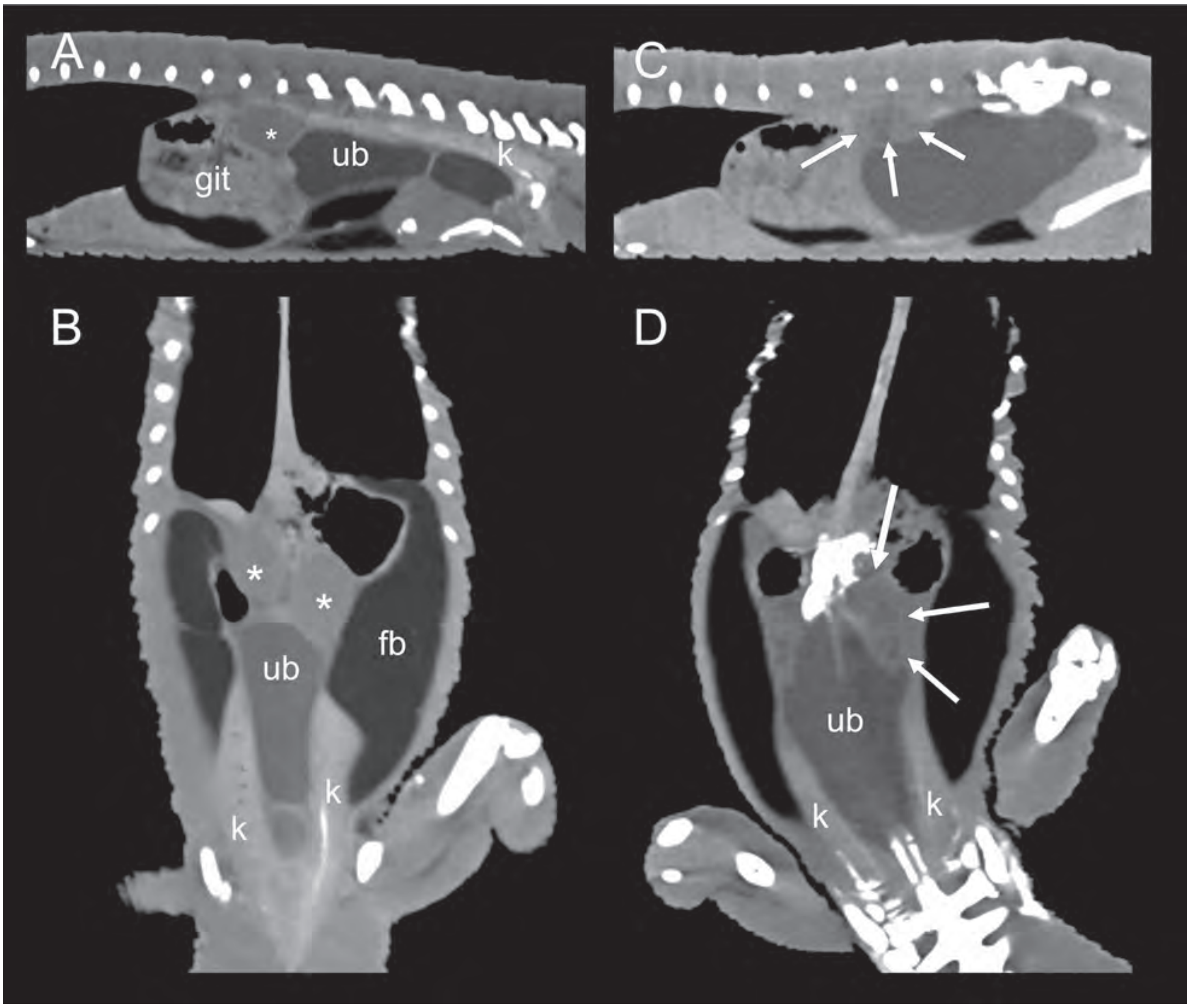

Figure 3. Sagittal (**A, C**) and coronal (**B, D**) contrast enhanced CT in adapted soft tissue windows of **A, B.** A male (ID 142) and **C, D.** A female (ID 366) *Dracaena guianensis*. The testis (asterisk) of the male individual appear as soft tissue dense (mildly hypodense to muscle tissue) homogeneous ovoid structures in the dorsal half of the mid-coelom. The ovaries (arrows) consist of multiple, grape-like positioned, small nodular hypodense structures surrounded with a contrast enhanced hyperdense wall or rim. fb - fat body, k - kidney, ub - urinary bladder-like structure, git - gastrointestinal tract.

D. paraguayensis. Likewise, the origin of these sexually dimorphic scales is still unknown despite their presence in a great number of species. (Lovern et al. 2004; Harvey et al. 2012) and so is their function. How could lizards benefit from displaying sex-dimorphic characteristics? Morphological traits or ornaments differing among sexes are usually used for courtship, agonistic behavior or communication in lizard species (Watkins 1998; Iraeta et al. 2011; Johnston et al. 2012). Prominent examples come from male anoles (*Anolis* spp.) using colored dewlaps in conjunction with head bobbing displays during courtship, whereas females rarely or never perform this behavior (Jenssen et al. 2000; Lovern et al. 2004). Similarly, rostral appendages or horns occurring in only a few lizard groups (Johnston et al. 2012) are suggested to provide information about male quality for both sexes (Whiting et al. 2015), mate or rival recognition (Rand 1961; Johnston et al. 2012), and are used in males fighting in territorial species (Čerňanský et al. 2014; Whiting et al. 2022). Concerning the comparatively inconspicuous position and size of scales in *D. guianensis*, we suggest that none of the above-mentioned signal characteristics can be affirmed for the scales in our study species. It is unlikely that conspecifics detect scale differences in juveniles as they mostly blend into the appearances of surrounding scales. The visual detection in adult male scales can, however, not be fully neglected. During basking, the postcloacal male buttons of adults are recognizable to human observers and potentially also to conspecifics. Adult male scales also show some degree of reflectance when observed under UV light (personal observation by the authors). Scales could also play a role in pheromonally mediated behaviors or serve as scent glands. We did not test visual or chemical signal function of scales in our current study, but it is something that could be looked at in future studies.

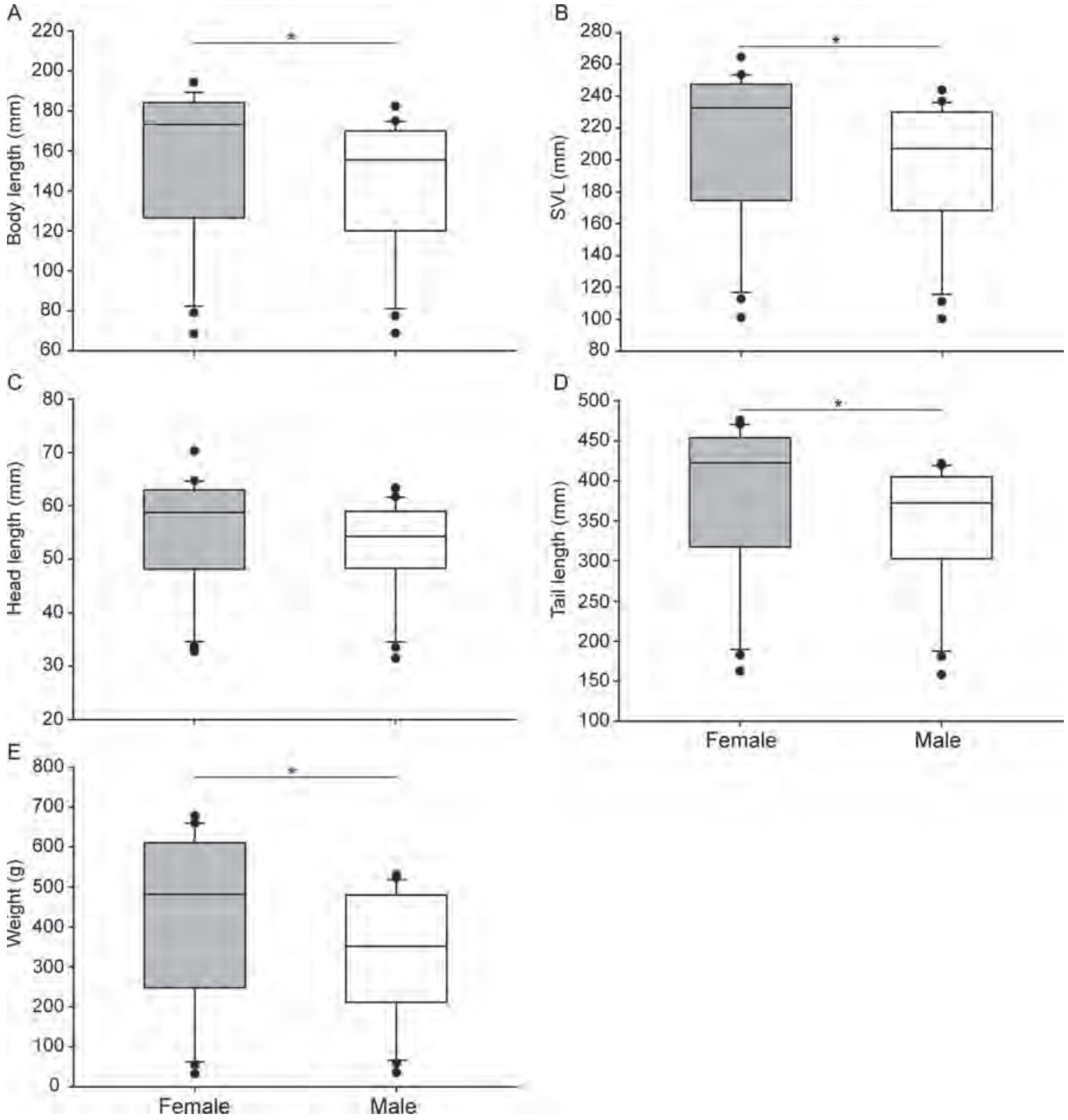

Figure 4. Size and weight differences of *Dracaena guianensis* juveniles. Boxplots show mean individual values of female (n=4) and male (n=4) sexed according to CT-scans and scales for a period of 21 month after hatching, with interquartile range, minimum and maximum values. Points designate outliners. Asterisk denote p-values from GLMMs.

Contrary to other studies where males were bigger than females (Rehak 1999; Mesquita et al. 2006; Frýdlová and Frynta 2015), we found no significant differences in SVL or other morphological parameters between adult males and females of the northern caiman lizard. Overall, lizards in the Teiidae family show a male-biased SSD (Anderson and Vitt 1990; Santana et al. 2010). Males of tegus (*Tupinambis* spp.) even show an enlarged jaw musculature during the reproductive season (Fitzgerald et al. 1991; Naretto et al. 2014) increasing bite performance, with the benefit of a stronger grip on a female to copulate, or dominating fights with other males (Naretto et al. 2014). Individuals at the Vienna Zoo rarely display dominant behavior. Males do not fight or behave aggressively if held together in a terrarium. Agonistic behavior has been reported in females from the Prague Zoo, but dominance patterns between conspecifics are scarce. When sexual selection on body mass is low or absent, males may benefit by maintaining a relatively light body, allowing them to be more mobile, and spend more time and energy on searching for mates instead of food (Trivers 1976). This is typical in lizard populations where densities are low and females are widely dispersed, thereby male mating success could depend on the number of females encountered rather than on competitive advantages over other males (Zamudio 1998).

In *D. guianensis*, we found morphometric differences between juveniles according to their sex classified by the sex-dimorphic scales. Female juveniles had a larger SVL, body length, tail length, and higher weight. In several species of lizards, skinks, and geckos the tail is also considered energetic storage and correlates with fat reserves

(Clark 1971; Roig and Carretero 2000; Sanggaard et al. 2012; Cardozo et al. 2015). The longer SVL in juvenile females resulted from longer body length, as head length did not differ compared to males. Female lizards might invest more energy in mass and length which in turn could increase their chances to breed earlier and reach relatively high fecundity (Yang et al. 2019), considering a pressure for fecundity selection (Olsson et al. 2002; Cox et al. 2003; López Juri et al. 2018), where large female body size allows the production of larger clutch size (Winck and Rocha 2012).

Conclusion

The current study provides the first evidence that juveniles can be sexed by sexually dimorphic bilateral scales, providing a non-invasive method to sex individuals rapidly at any life stage. We further show that SSD exists in juveniles during ontogenetic development, however, this SSD disappeared in adults. Hence studying differences and similarities of morphometric parameters between the sexes during development and in correlation with behavior, clutch size, and associated reproductive success might help to understand selection factors promoting SSD in different life stages.

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Supplementarymaterial1

[illegible] *Dracaena guianensis* [illegible]

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Data type: docx

Explanation note: Data are estimated means ± standard error (SE) and P-value of generalized linear mixed models (GLMM). 21 measurements for juveniles, nine for adults. Sex was assigned according to CT scans or a reproductive event (see Table 1) excluding juveniles: 924, 926 and 929, or adults: 368 and 369; sample sizes in parentheses.

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