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The Morphology of *Sphaerodactylus nicholsi* × *Sphaerodactylus townsendi* (Gekkota: Sphaerodactylidae)

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Biological research has long investigated hybridization and introgression between species. Hybrid zones in squamates are rare relative to many other vertebrate groups and are exceptionally rare in gecko lizards. A notable exception is the stable hybrid zone in mid-coastal areas of southern Puerto Rico between the gecko species *Sphaerodactylus nicholsi* and *S. townsendi*. Forty years ago, hybridization between these species was reported using electrophoretic data, and this hybrid zone was recently re-described using genetic sequence data. Even though this hybrid zone is relatively well documented, the phenotypic changes associated with this evolutionary event have not been reported in detail. Here, we examined 14 scalation and pigmentation characters and 15 skeletal measurements in all putative hybrid specimens, as well as variation in both parental species, to describe hybrid morphology. Results show a large amount of overlap between the parental species and the putative hybrids. However, we did observe surprising differences in some skeletal proportions and external characters that are potentially physiologically relevant. Because there is no evidence of intermediate habitat spanning the hybrid zone and both species possess strong evidence of niche overlap, deviations from the parental phenotype may be maladaptive, thus providing a testable hypothesis for why hybrid genotypes may be selected against in this region. As the only geographically stable hybrid zone previously described with genetic sequence data in gecko lizards, this concomitant morphological description is crucial to a better understanding of this system and—by extension—hybridization across vertebrates.

REPRODUCTIVE isolating mechanisms are not always impermeable and allow the crossing of individuals that differ from each other genetically and taxonomically (Darwin, 1859; Mayr, 1970). Hybridization is well known across animal groups (Schwenk et al., 2008), ultimately catalyzing evolution and increasing diversity (Barton, 2001; Shang and Yan, 2017). Geographical regions where hybridization occurs—hybrid zones—may be temporary, as this phenomenon is often prevented by prezygotic and postzygotic barriers, with hybrid offspring generally having reduced fitness (Dobzhansky, 1940; Barton and Hewitt, 1985). However, many cases of stable hybrid zones have also been reported (Moore, 1977; Schwenk et al., 2008; Stöck et al., 2021). Hybridization is widespread across vertebrates, but there is a dearth of robust examples across squamates, particularly within gecko lizards (Pinto et al., 2019). The persistence of hybrid zones can generally be explained by two non-mutually exclusive mechanisms: selection for hybrid phenotypes in a region of intermediate habitat, or a balance between parental dispersal and subsequent selection against hybridization (Moore, 1977; Barton and Hewitt, 1985; Pinto et al., 2019). In many cases, both mechanisms appear to be involved in the formation and maintenance of hybrid zones (Barton and Hewitt, 1985).

The main island of Puerto Rico harbors seven described species of geckos within the genus *Sphaerodactylus*, including *S. gaigeae*, *S. grandisquamis*, *S. klauberi*, *S. nicholsi*, *S. roosevelti*, *S. townsendi*, and *S. verdeluzicola* (Fig. 1).

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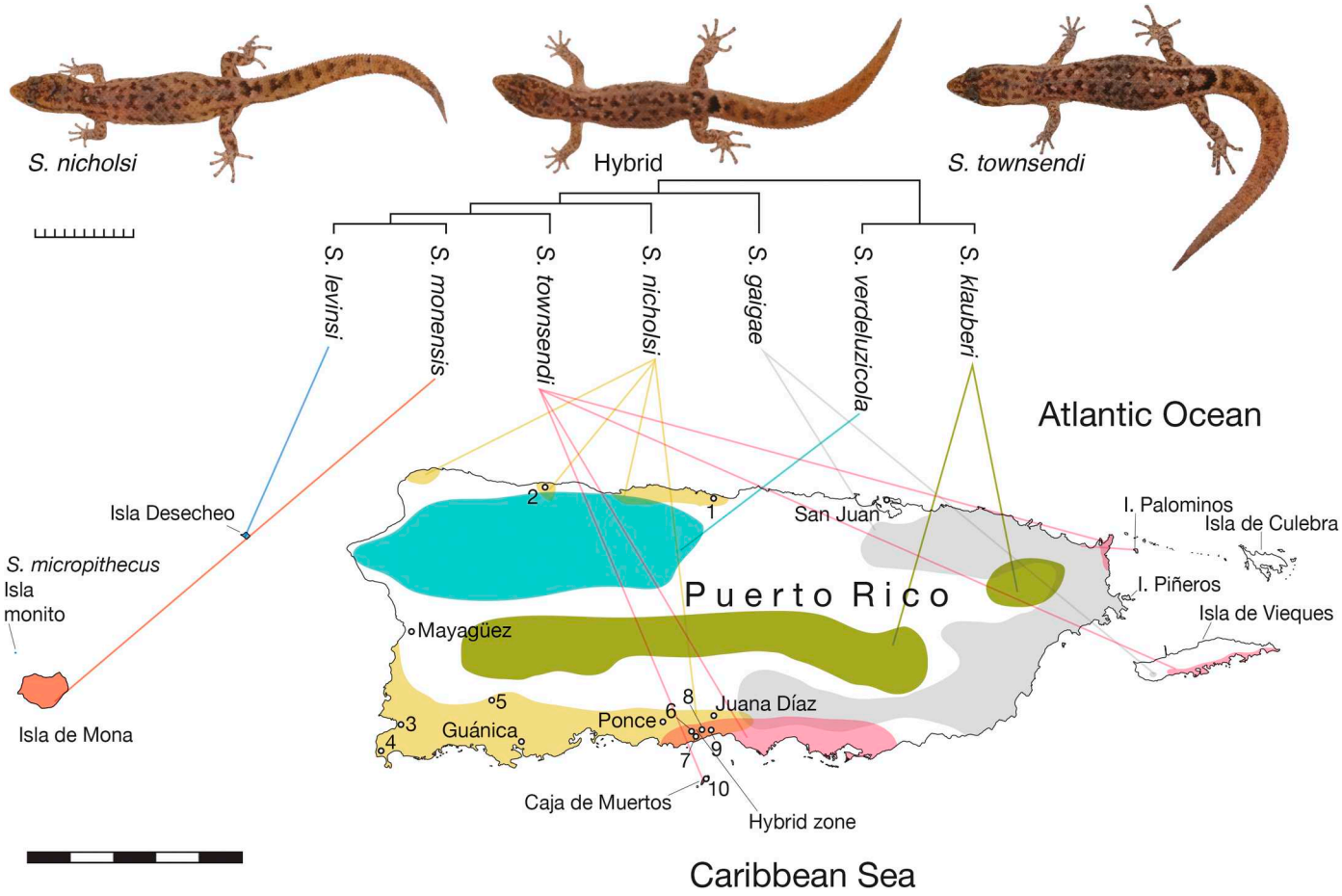

Fig. 1. Distribution map of *Sphaerodactylus nicholsi*, *S. townsendi*, and closely related species from the Greater Puerto Rico area. The hybrid zone of the focal species is the overlapping dark area between yellow and pink. Numbers on the map correspond to specimen localities: 1, Manatí; 2, Camuy; 3, Cabo Rojo; 4, Cabo Rojo; 5, Sabana Grande; 6, Ponce; 7, Ponce; 8, Juana Díaz; 9, Juana Díaz; 10, Caja de Muertos. Molecular cladogram adapted from Díaz-Lameiro et al. (2022). Upper scale bar = 10 mm; lower scale bar = 50 km.

Sphaerodactylus nicholsi is the smallest species on the island (mean SVL = 24.5 mm), occurring in the coastal areas of the northwest of Puerto Rico and in the southwest to approximately the area of Santa Isabel. *Sphaerodactylus townsendi* is slightly bigger (mean SVL = 28.0 mm), occurring in the southeast, from Santa Isabel to around Maunabo with isolated populations occurring on satellite islands beyond mainland Puerto Rico (Schwartz and Henderson, 1991). *Sphaerodactylus nicholsi* and *S. townsendi* have been erroneously regarded as allopatric (Grant, 1931) or two subspecies of *S. nicholsi* (Thomas and Schwartz, 1966), and hybridization or intergradation between these species had been suspected (Thomas and Schwartz, 1966; Schwartz and Thomas, 1975). A hybrid zone was later confirmed, with 88% of sampled animals showing signs of hybrid ancestry at a specific location in southern Puerto Rico (Murphy et al., 1984). The parental species occur in coastal habitats that range from 17 to 50 centimeters of annual rainfall (NOAA, 2025), occupying moist-alluvial habitats in the northwest and southwest (*S. nicholsi*), and in the northeast *(S. townsendi*) part of the island. In general, *S. townsendi* inhabits somewhat less arid situations than *S. nicholsi* (Thomas and Schwartz, 1966). In the mid-south region, including the hybrid zone, these species occupy areas classified as dry-alluvial (Helmer et al., 2002). The hybrid zone falls within the municipality of Juana Díaz (Thomas and Schwartz, 1966; Schwartz and Thomas, 1975), specifically, a semi-arid coastal plain with no apparent topographic barriers separating the parental species, although annual precipitation and corresponding physiological demands might be relevant as this region hosts a hot, dry climate with high rates of evaporation through the year (Ramos-Ginés, 1994; Colón Torres, 2009). The stability of the hybrid zone between these species was recently confirmed using molecular sequencing of both hybrids and parental species (Pinto et al., 2019). Also, the hybrid zone is not exclusively occupied by hybrids, but individuals from parental species are found there too.

While *S. nicholsi* and *S. townsendi* are very similar morphologically, occupy similar fundamental niches, possess very similar color patterns (Figs. 2–3), share the same sex chromosome system, and their distribution ranges overlap in the mid-south coastal regions of Puerto Rico, these two species are not sister taxa (Díaz-Lameiro et al., 2013; Pinto et al., 2019, 2022; Fig. 1). In previous studies, it has been reported that these hybrid *Sphaerodactylus* may exhibit slight phenotypic differences from the parental species (Murphy et al., 1984; Pinto et al., 2019; Fig. 4). However, the morphology of the hybrids has not been formally described in detail (but see Thomas and Schwartz, 1966). Here, we describe the morphological variation of *S. nicholsi* and *S. townsendi*, compared with

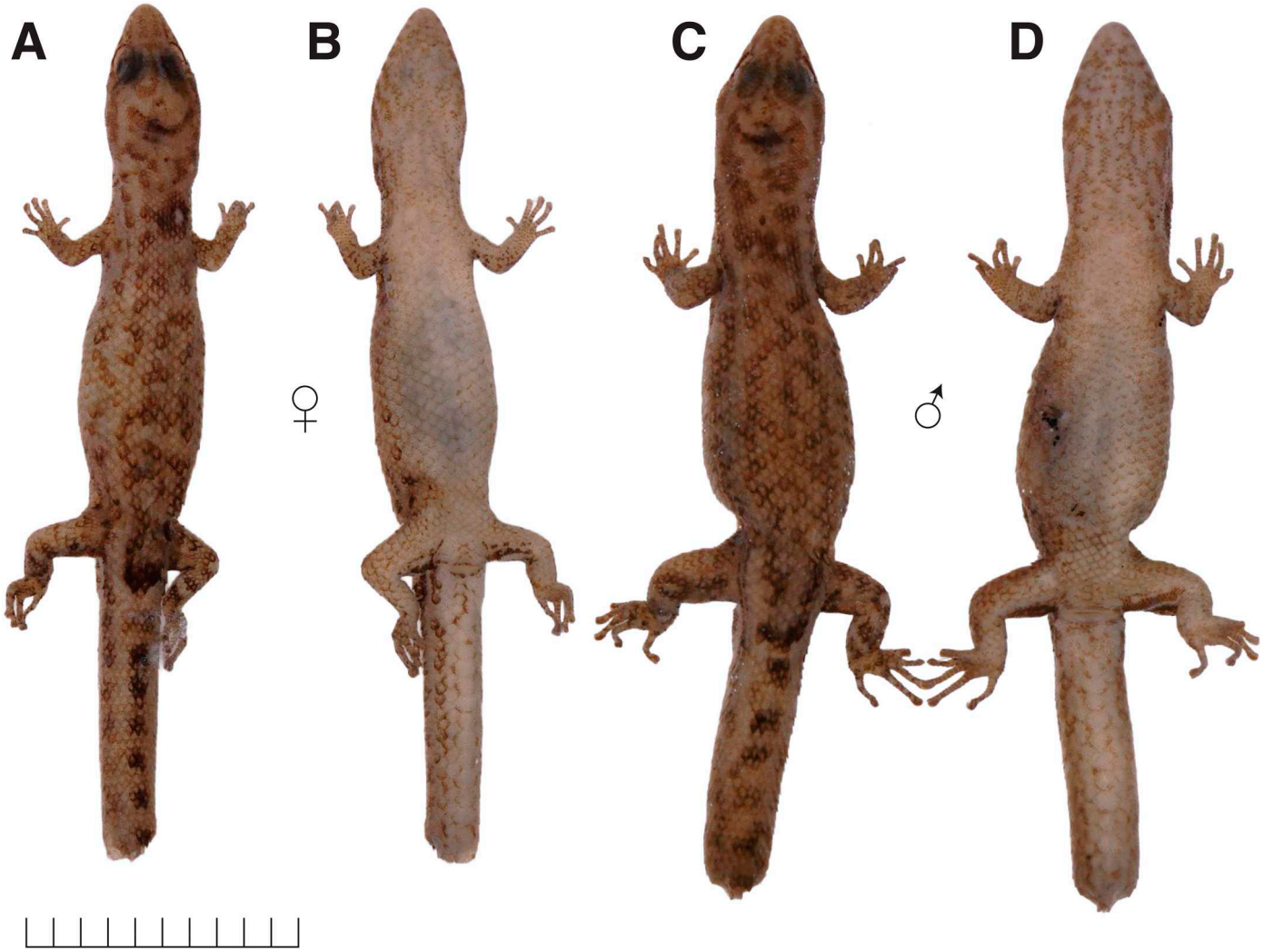

Fig. 2. Body coloration of *Sphaerodactylus nicholsi* from the locality of Cabo Rojo, Puerto Rico. (A–B) Female specimen (RT 14650); (C–D) male specimen (RT 14649). (A, C) Dorsal view; (B, D) ventral view. Scale bar = 10 mm.

putative hybrids. We looked at 14 external characters and 15 skeletal measurements to describe the morphology of *S. nicholsi* × *S. townsendi* hybrids. The results allow us to characterize the phenotype of the putative hybrids and to determine which osteological features may be affected by hybridization.

MATERIALS AND METHODS

The groups analyzed were determined based on distribution and external morphology (Grant, 1931; Thomas and Schwartz, 1966; Schwartz and Henderson, 1991; Henderson and Powell, 2009). In our analysis, we consider to be putative hybrids only individuals collected in the hybrid zone (Murphy et al., 1984; Pinto et al., 2019) that lacked diagnostic characteristics of the parental species, e.g., *S. nicholsi* small (SVL in males to 24 mm, in females to 25 mm) with crescentic cephalic figure and well-defined scapular patch with paired ocelli, vs. larger *S. townsendi* (SVL in males and females to 28 mm) and lack the crescentic cephalic and scapular patch (Grant, 1931; Thomas and Schwartz, 1966). Additionally, one of the hybrid specimens was confirmed previously with genetic sequence data (Pinto et al., 2019). To compare putative hybrids and non-hybrids, we used 15 morphological characters (Fig. 5) assessed using a Leica MS5 dissecting microscope, and a Keyence Digital Microscope VHX-7000 series using the autofocus option or the 3D stitching function.

The characters examined here were used in previous descriptions (Grant, 1932; Thomas and Schwartz, 1966; Daza et al., 2019): 1) crescent shape on the back of the head (present/absent), 2) crescent shape meets the postocular line (present/absent), 3) chin pattern (plain, spots, streaks, mottling), 4) speckled chin background (present/absent), 5) chin scales (keeled/smooth), 6) collar scales (keeled/smooth), 7) chest scales (keeled/smooth), 8) snout scales (keeled/smooth), 9) snout scales (regular, irregular), 10) dark line posterior extension (no line/reaching the tympanum/beyond the tympanum), 11) postocular line (absent/extended to tail/only in tail), 12) number of dotted lines on back (0/2/4/5), 13) scapular patch (present/absent), 14) scapular patch encircled by dark margin (present/absent), 15) sacral pattern shape (no pattern or blotch/U-shaped/V- or Y-shaped).

For the morphometric analysis, we analyzed skeletal data from 41 X-rayed specimens. Digital X-rays of the fixed specimens were obtained using a Thermo Scientific PXS5-927

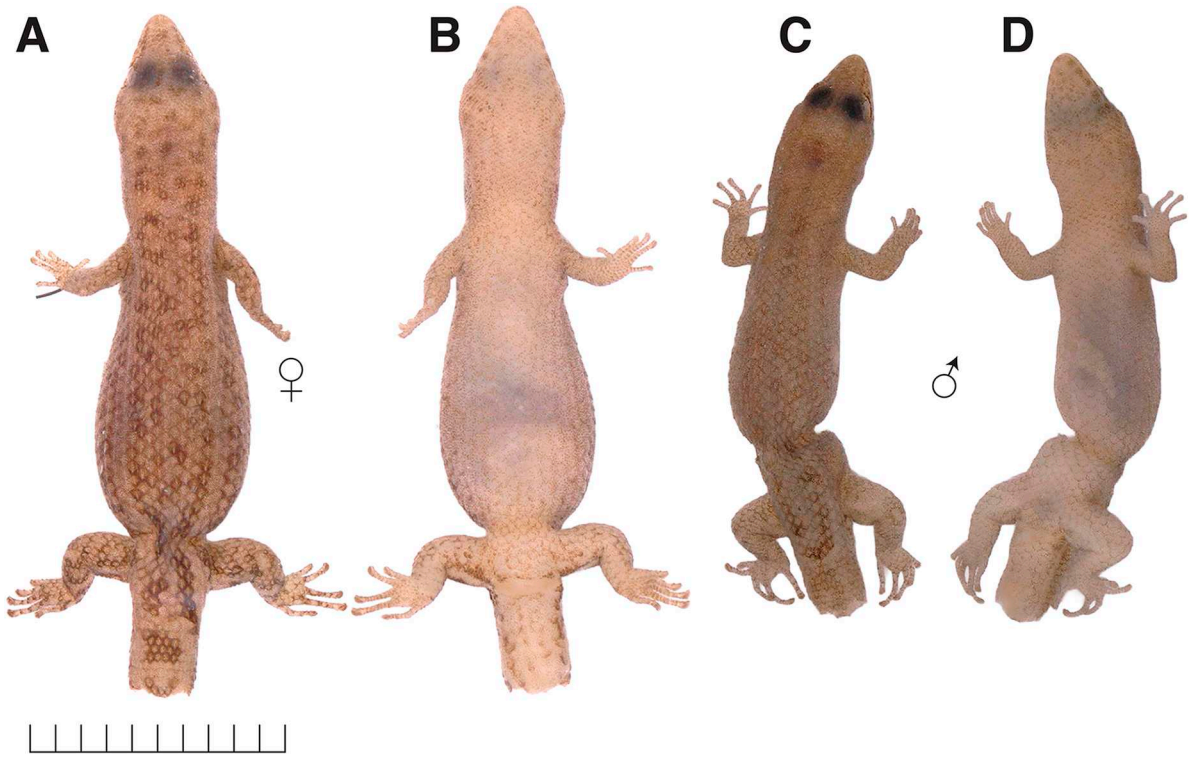

Fig. 3. Body coloration of *Sphaerodactylus townsendi* from the locality Isla Caja de Muertos, Puerto Rico. (A–B) Female specimen (TG2019); (C–D) male specimen (TG2060). (A, C) Dorsal view; (B, D) ventral view. Scale bar = 10 mm.

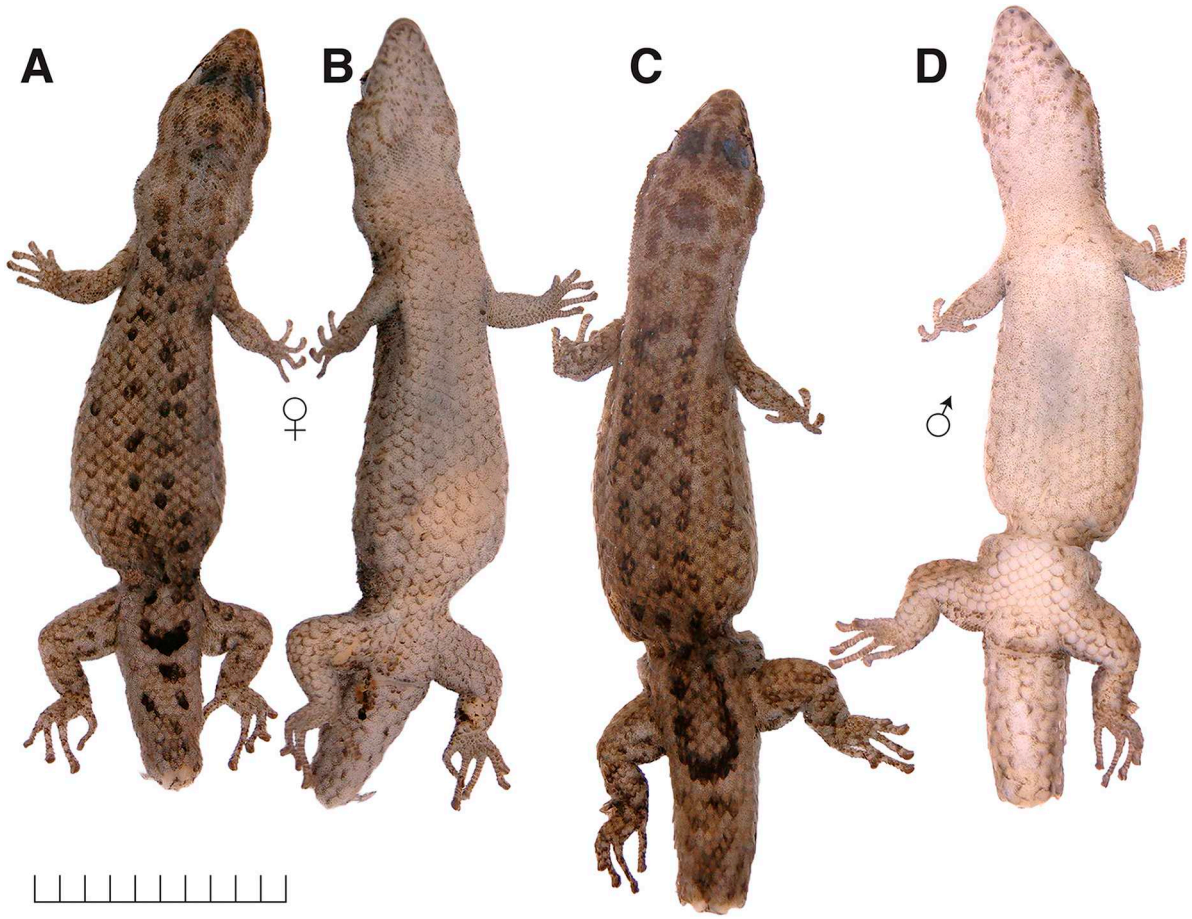

Fig. 4. Body coloration of the putative *Sphaerodactylus nicholsi* × *S. townsendi* hybrids from Juana Díaz, Puerto Rico. (A–B) Female specimen (JDD 00372); (C–D) male specimen (JDD 00373). (A, C) Dorsal view; (B, D) ventral view. Scale bar = 10 mm.

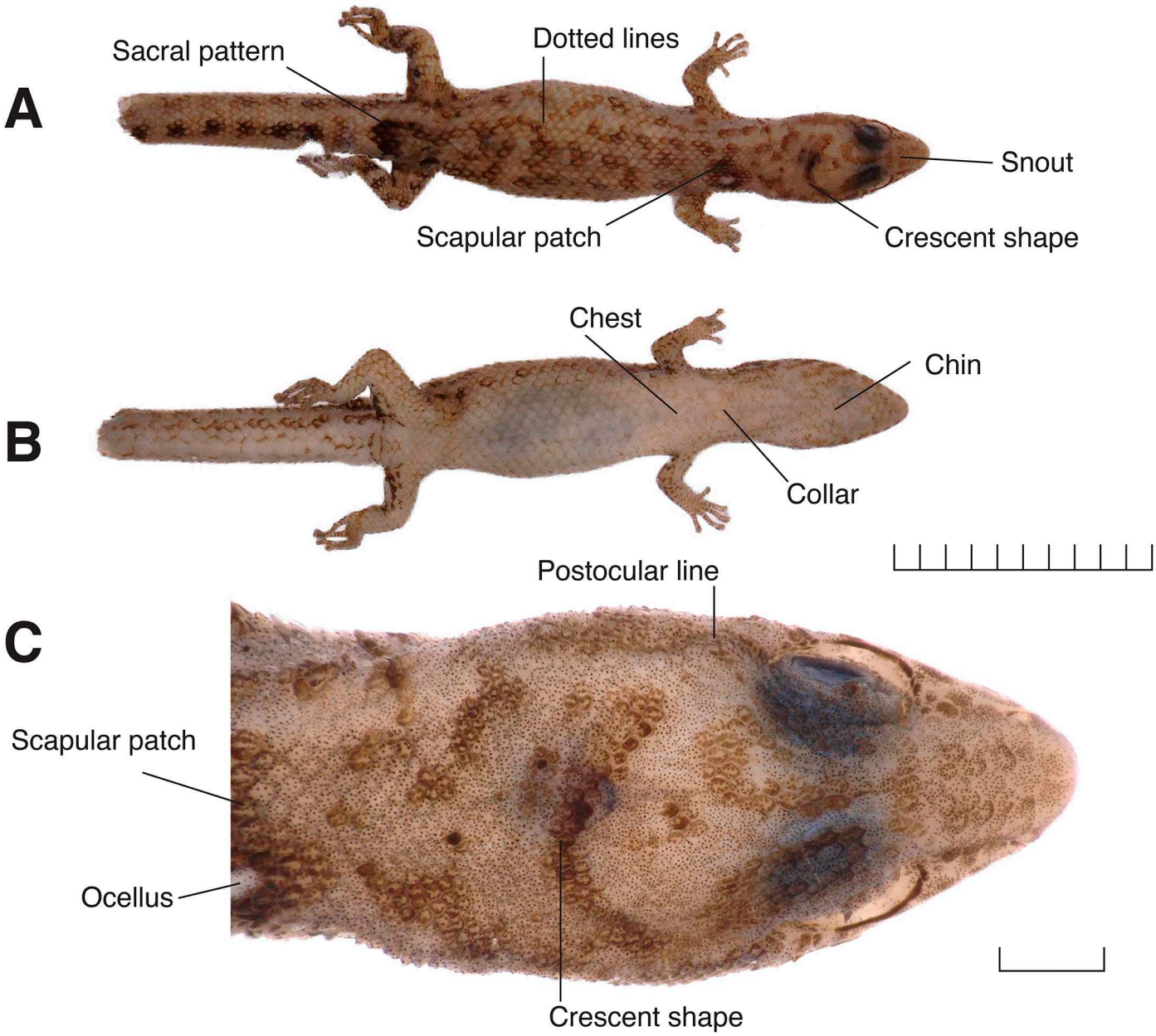

Fig. 5. Body coloration characters used in this study indicated in one female specimen of *S. nicholsi* (RT 14650). (A) Full body dorsal view; (B) full body ventral view; (C) close up of head and neck dorsal view. Scale bar for A and B = 10 mm; scale bar for C = 1 mm.

microfocus X-ray source and a Mars 1717 V Wireless a-Si Flat Panel Detector. A radiopaque ruler was included on the X-rays for the scale, and scotch tape was applied to maintain the specimen straight when needed. Measurements were taken on X-rayed specimens using ImageJ (Schneider et al., 2012). One specimen was CT scanned to show better the measurements taken on the X-rays at the University of Texas at Austin–High-Resolution X-Ray CT Facility (Fig. 6).

The following measurements were taken on 19 specimens of *S. nicholsi*, 11 specimens of *S. townsendi*, and 11 putative hybrids: 1) snout to vent length, 2) skull length, 3) skull width, 4) humerus length, 5) ulna length, 6) fourth manual toe length, 7) femur length, 8) tibia length, and 9) fourth pedal toe length. These measurements were taken on both sides, three times, and the mean value calculated. For measurements that have left and right values, we selected the highest value to try to minimize errors caused by the angle of the element in the specimen (i.e., a bone can be seen very short on an X-ray if it is not horizontal, but oblique oriented).

A principal component analysis (PCA) was performed to find if there are morphometric differences among the three groups included. The PCA was performed in R v4.6.0 (R Core Team, 2025), using the package factoMineR (Lê et al., 2008), and graphs were created using the package ggplot2 (Wickham, 2016). Boxplots for all the continuous variables were created to show the differences between the parents and the putative hybrids. We also test for normality of the data before performing statistically significant differences tests. One-way ANOVAs were performed for normally distributed variables, while Dunn's multiple comparisons test was performed on the non-parametric variable (see Results).

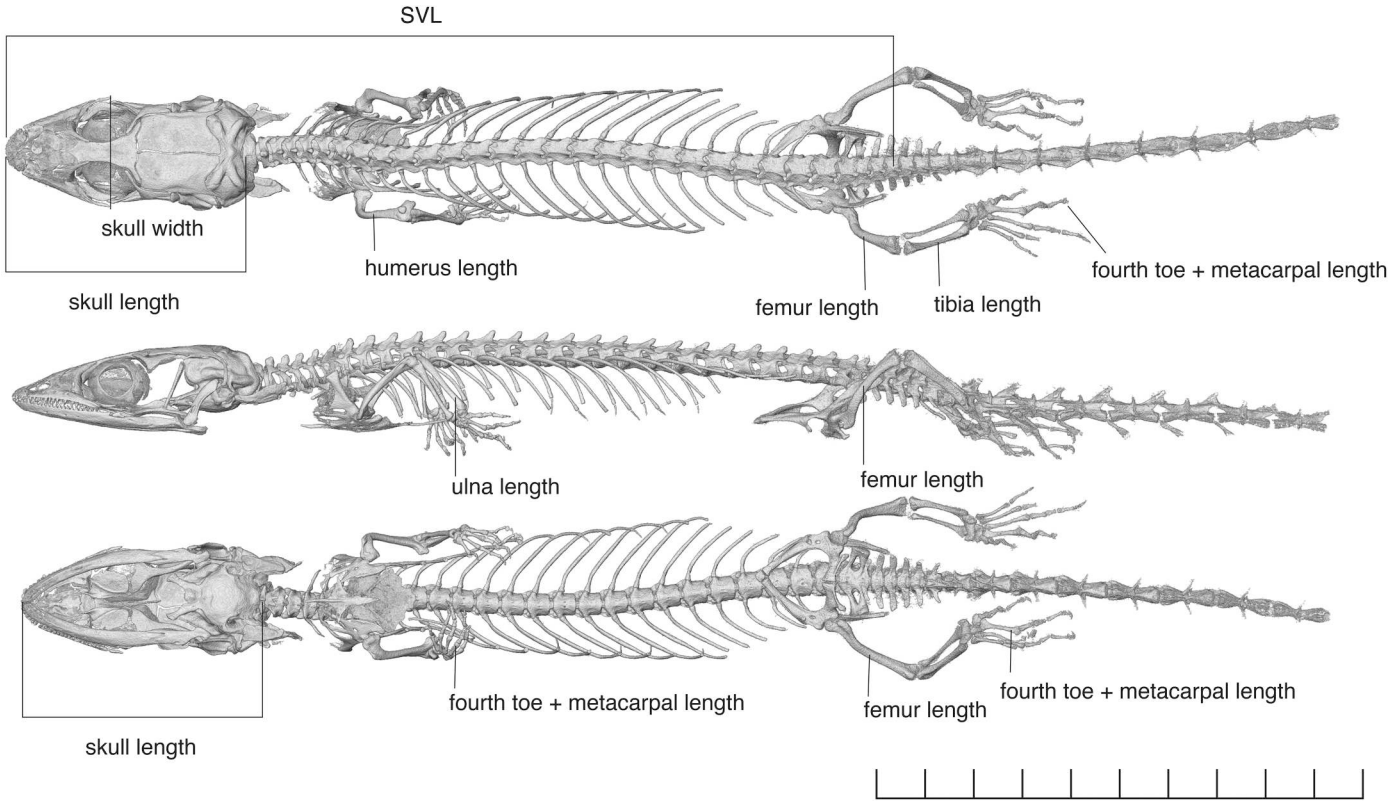

Fig. 6. Skeletal data measurements indicated in an HRCT of *Sphaerodactylus nicholsi*. Scale bar = 10 mm.

All boxplots, statistical analysis, and bar diagrams were done using GraphPad Prism version 10.42 for Mac OS (Boston, Massachusetts, USA; https://www.graphpad.com). All data are included in the supplementary file (see Data Accessibility).

RESULTS

External morphology.—For each external character, we calculated the percentage of the specimens exhibiting the different character states (Fig. 7). From the 15 external pattern characters evaluated, characters 4, 5, 7, and 8 were constant in all specimens: 4) presence of speckled chin background, 5) chin scales keeled, 7) chest scales smooth, and 8) snout scales keeled.

The presence of a crescent shape on the back of the head (Character 1) is mainly present in specimens of *S. nicholsi* (95.34%) and a few hybrids (23.07%) but is absent in *S. townsendi*. The crescent shape can be wide, in which case it meets the postocular stripes, or narrow and not contacting the stripes (Character 2). For this trait, 83.72% of *S. nicholsi* and only 15.38% of the hybrids showed the crescent shape contacting the postocular stripe, indicating that the crescent shape tends to be narrower in the hybrids. The pigmentation pattern of the chin (Character 3) is variable among the groups and within the groups (plain, spots, or streaks); however, no specimens of *S. townsendi* had a plain chin, and 44.44% of them showed a mottling pattern not seen in other groups. The presence of keeled scales in the collar (Character 5) was absent in all the hybrids, but present in both parental species (Fig. 8). The width of the snout scales was almost invariable, with specimens showing uniform scales, but a few individuals of *S. nicholsi* have irregular size scales (4.65%). Dark line posterior extension (Character 10) and sacral pattern (Character 15) were variable among all groups. All groups have stripes down their back, extending from the top of the head to the tail or sacral area (Character 12). These lines are made up of many dots that define a striped pattern, but the number of lines differ in each specimen and between species. *Sphaerodactylus nicholsi* and *S. townsendi* have few specimens with few or no lines, with most individuals having four or five lines. Finally, a faint scapular patch is present in all the groups but is more defined in *S. nicholsi* (51.12%), especially in specimens from the northern populations, and rarer in the hybrids (15.38%). When the scapular patch was present, it was encircled by a dark margin in most *S. nicholsi* (44.18%) and less frequently in the hybrids (12.38%). The postocular line (Character 11) appears as a white or tan stripe that begins behind each eye and runs down the back along the sides of the animal. The extension of this line, or the location on the body where it comes to an end has been traditionally used to characterize these species. The postocular line varies among the groups, it extended to the tail in most of the specimens of each group, being restricted to the tail in only a few of them (*S. nicholsi* 9.3%, *S. townsendi* 11.11%, and hybrids 7.69%). A postocular line extending to the tail is more frequent in hybrids (92.3%).

Linear morphometrics.—All the continuous variables passed four normality tests (D'Agostino and Pearson, Anderson-

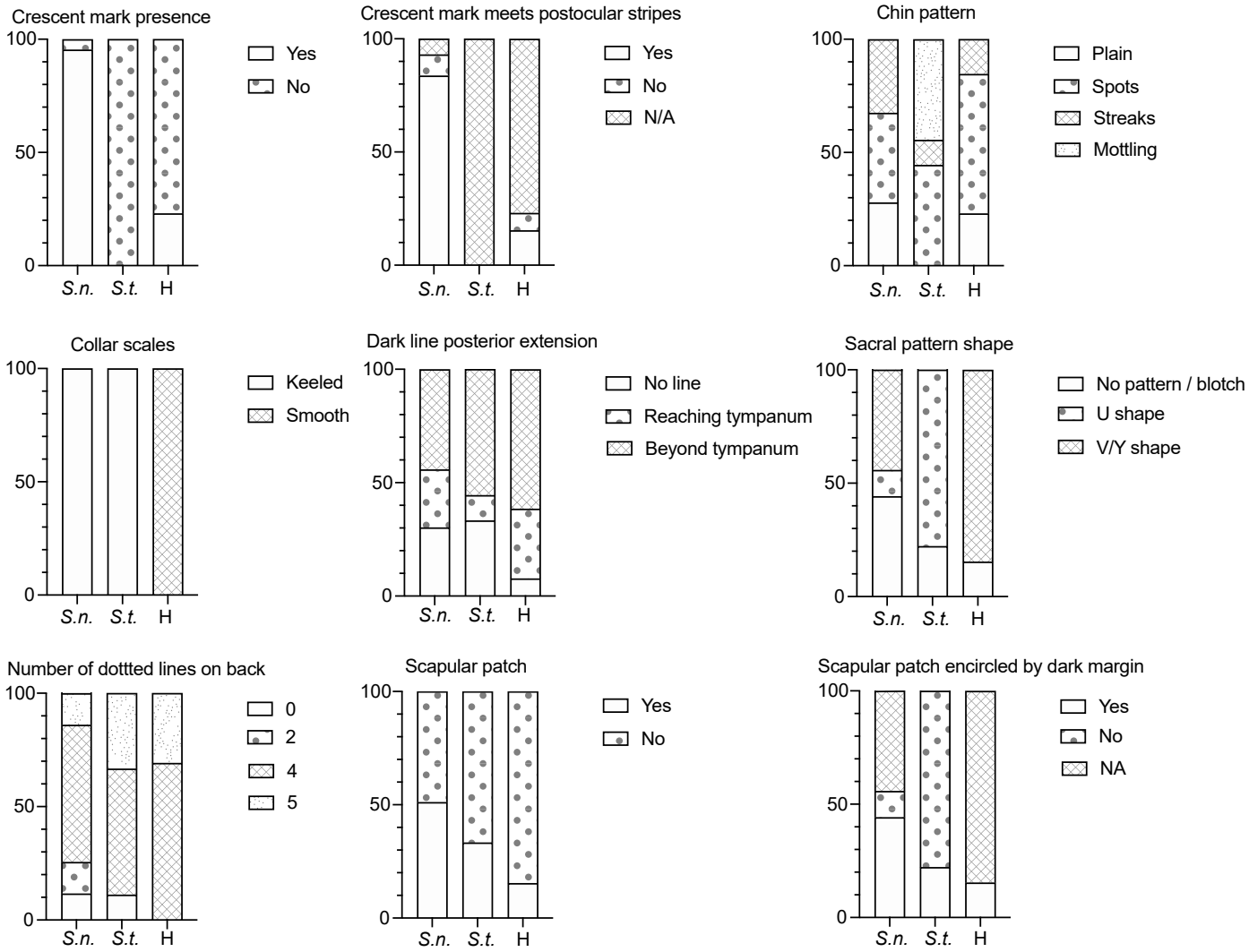

Fig. 7. Variation in external characters; constant characters not shown. The percentage of each character state in the sample was calculated. *S.n.* = *Sphaerodactylus nicholsi*; *S.t.* = *Sphaerodactylus townsendi*; H = putative *S. nicholsi* × *S. townsendi* hybrids.

Darling, Shapiro-Wilk, and Kolmogorov-Smirnov), except the 4th toe in the forelimb. One-way ANOVAs were performed for skull length, skull width, SVL, humerus length, ulna length, 4th toe in the hindlimb, femur length, and tibia length. A non-parametric Dunn's multiple comparisons test was performed for the 4th toe in the forelimb, showing significant differences between *S. nicholsi* and *S. townsendi* ($P = 0.0004$), and *S. nicholsi* and hybrid ($P < 0.0001$).

The distribution of linear measurements indicates that median values of five measurements (except humerus, ulna, femur, and tibia lengths) were higher in the hybrids. These values derived from the stylopodium (humerus and femur) and zeugopodium (ulna and tibia) are prone to be affected by the preservation pose of the specimen (see discussion). In any case, the hybrids are more similar in skeletal proportions to *S. townsendi* than to *S. nicholsi*. Likewise, hybrids tend to have larger heads than the two parental species (as indicated by skull length and width; Fig. 9).

The principal component analyses of all 15 skeletal measurements combined yield a plot where the three groups overlap (Fig. 10). PC1 (69% of the variation) is explained mainly by the femur (14.06%), SVL (13.68%), 4th toe forelimb (12.55%), skull width (12.24%), and skull length (12.07%). PC1 indicates that *S. nicholsi* is smaller, has smaller and narrower skulls, and shorter front 4th toe. On the other extreme of the variation, the hybrids have larger femora, and larger and wider skulls, despite being smaller than *S. townsendi*. PC2 (11.7%) is explained mainly by humerus length (43.49%) and ulna length (25.48%), indicating that the hybrids tend to have shorter humeri and ulnae. However, this result is less significant given the low percentage of explanation of PC2 and the measuring error affecting values from these bones.

DISCUSSION

Sphaerodactylus townsendi, although described as separate species (Grant, 1931), was later synonymized as a subspecies of *S. nicholsi* (Thomas and Schwartz, 1966) and elevated to full species by Schwartz and Henderson (1988). The earliest mention of the hybrids from Juana Díaz was done by Thomas and Schwartz (1966), and they considered this population as intergrades with no cephalic

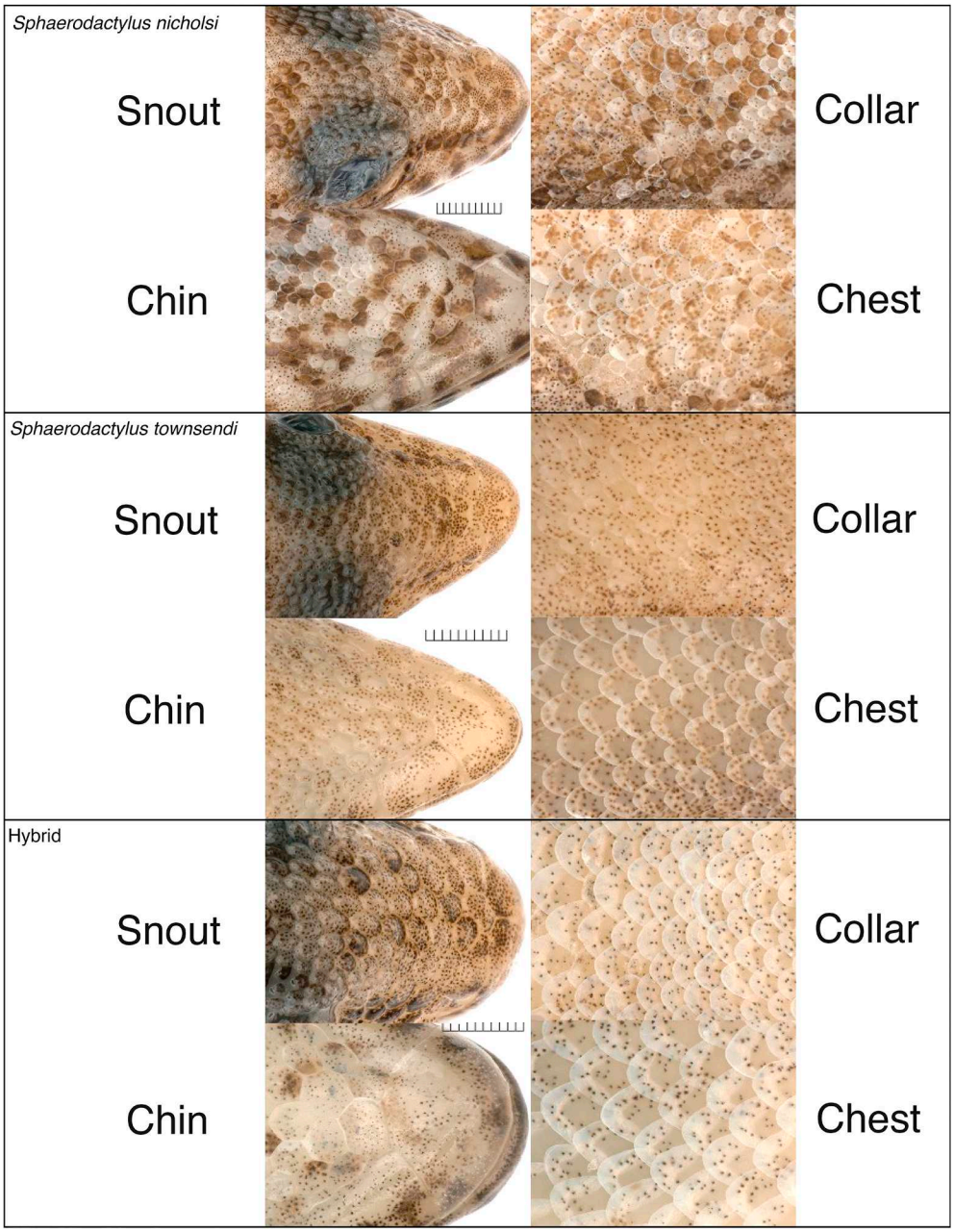

Fig. 8. Close up of selected regions of the integument to show the scales in *Sphaerodactylus nicholsi* (RT 14654), *S. townsendi* (TG2019), and a hybrid specimen (TG3172). Scale bars = 1 mm.

crescent and larger size. The results from the external morphological characters and linear morphometrics indicate that *S. nicholsi* and *S. townsendi* indeed share several morphological similarities and overlap considerably. Although these species are genetically distant, and not each other's closest relatives, they are capable of hybridizing and producing viable offspring that exhibit a combination of characters of both parental species. Hybrid morphology in this group was poorly understood (e.g., Thomas and Schwartz, 1966), but this study indicates that putative hybrids are more like *S. townsendi* in external morphology, sharing the lack of the crescent-shaped mark, but differ from the two parental populations by their apparent lack of keeled collar scales ($n = 6$). Perhaps the most interesting change observed among hybrids is that they show an intermediate SVL between the parental species, and proportionally larger and wider heads and longer femora. The X-ray data were effective in demonstrating some of these osteological differences, but high-resolution CT (HRCT) data would be more accurate to eliminate the error caused by the preservation pose of the specimen—in 3D models, the bones can be visualized and measured from any angle, while in X-rays, the two dimensional view is limited by the orientation of bones (e.g., inclination of limbs or digits not fully extended). Despite the limitation by 2D X-ray data, these images are cost and time effective, especially when dealing with large series of specimens. We are confident that the observed differences in head proportions are less prone to measuring error, due to our optimized methodology (i.e., taping the specimen to the stage). We demonstrate that the putative hybrid population morphology is not just a

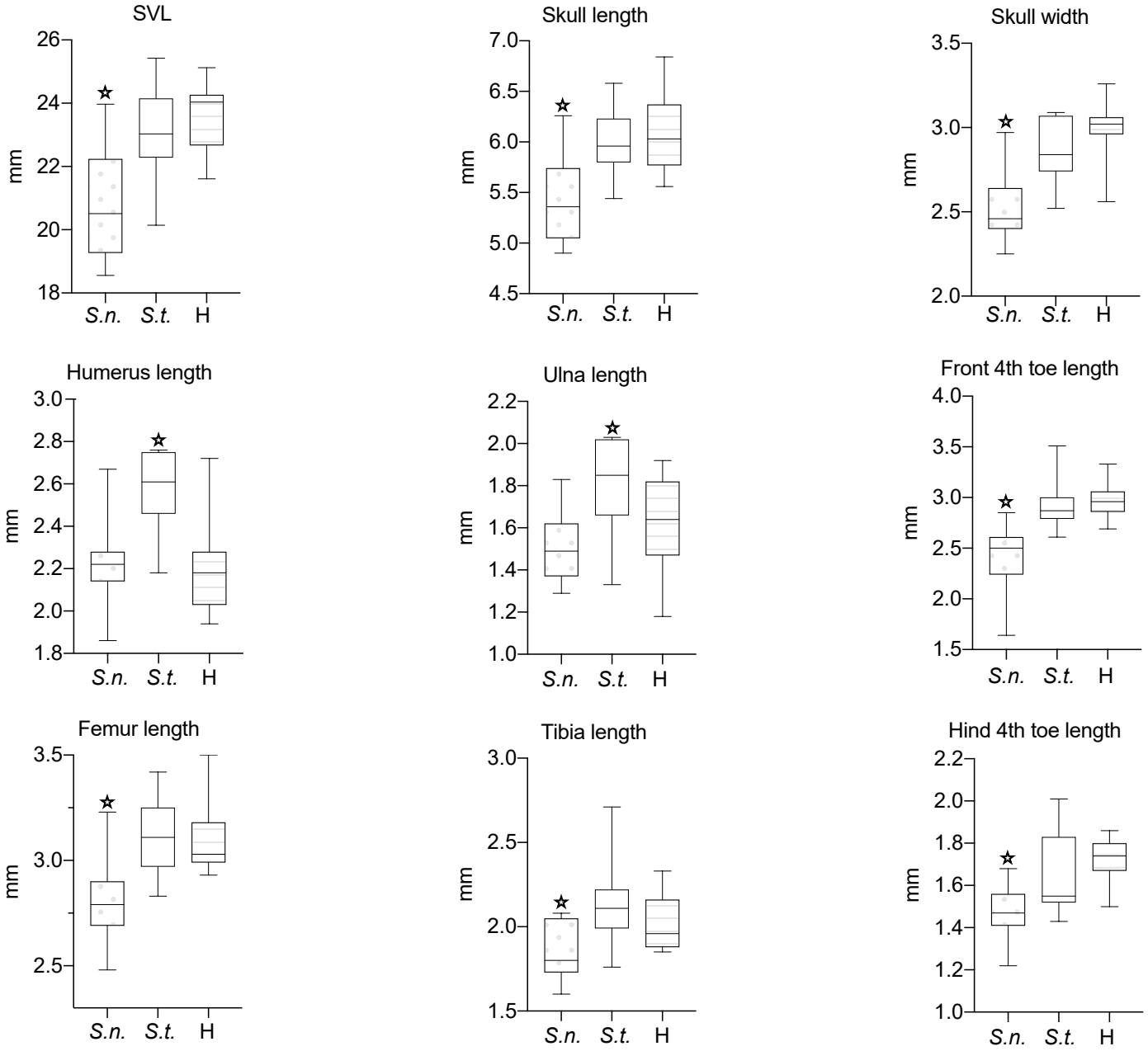

Fig. 9. Boxplots indicating the linear measurements of skeletal structures. Middle bar indicates median value. *S.n.* = *Sphaerodactylus nicholsi*; *S.t.* = *Sphaerodactylus townsendi*; H = putative *S. nicholsi* × *S. townsendi* hybrids.

blended phenotype, but instead, hybrid individuals can be recognized from the parental species by a combination of variable and unique phenotypic traits (e.g., hybrids with larger skulls and smooth collar scales). Most importantly, we find that there is not a single hybrid phenotype, but a range of hybrid phenotypes that overlap to varying degrees with the parental species, consistent with theory and empirical studies of hybrid zones in other taxa (Mayr, 1965; Barton and Hewitt, 1985; Pacheco-Sierra et al., 2016).

Finally, *S. nicholsi* and *S. townsendi* differ in the keeling pattern of the snout scales (absent in *S. townsendi* vs. present in *S. nicholsi*; Grant, 1931). We could not corroborate this character proposed almost 90 years ago, as all the specimens had keeled scales on the snout, even the hybrids. Grant was limited by optical technology available at that time (e.g., handheld microscopes or early dissecting microscopes), whereas we were able to find the keeled scales in *S. townsendi* when examining the specimens in a Keyence digital scope that can magnify the specimens up to 200X. However, even at this magnification, the keels are very faint. This is a good example of how technological advances can help refine our understanding of morphological variation.

Hybridization studies are important regarding not just our understanding of genetics, but also phenotypic differences. This work provides an in-depth morphological study of the first stable hybrid zone in geckos also investigated using genetic sequence data. Samples taken from the hybrid zone showed morphological differences when compared to either

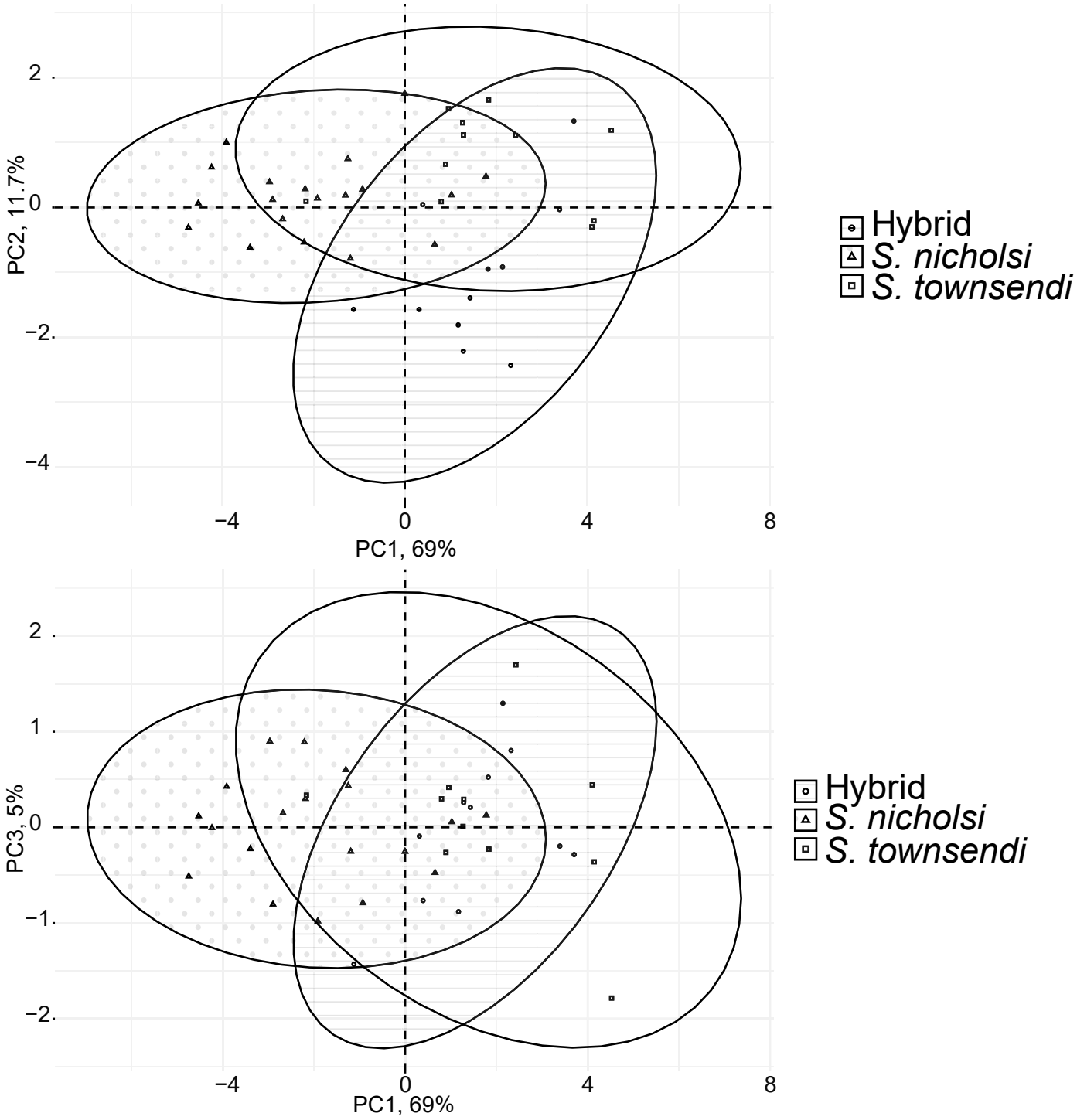

Fig. 10. Results from the principal component analysis. Ellipses were traced using the default function in factoMineR.

parental species. Previous work analyzing distributions of both parental species predicts, given large amounts of fundamental niche overlap, they should compete strongly with each other, were they to meet in a location without hybridization (Pinto et al., 2019). Selection against hybridization could be partially driven by these subtle morphological differences. Future work should focus on investigating putative physiological differences between parental species and their hybrid offspring optimally using controlled laboratory crosses to help control for genotypic variation.

DATA ACCESSIBILITY

Supplemental material is available at https://www.ichthyologyandherpetology.org/h2025061. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and

AI STATEMENT

The authors declare that no AI-assisted technologies were used in the design and generation of this article and its figures.

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