Surface sculpturing in the skull of gecko lizards (Squamata: Gekkota)

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Received 4 August 2020; revised 17 August 2020; accepted for publication 21 August 2020

It has previously been stated that geckos are characterized by smooth cranial bones bearing no sculpturing; however, there are many exceptions. Here we systematically characterize variation in sculpturing in cranial bones across all seven gekkotan families and examine patterns of evolutionary transitions in these traits on a multigene molecular gekkotan phylogeny to elucidate trends in phenotypic diversification in bone sculpturing. Over 195 species were reviewed using specimens where smooth, grooved, pitted and rugose sculpturing patterns were found. Of the 26 cranial bones, only seven (premaxilla, maxilla, nasal, prefrontal, frontal, parietal and postorbitofrontal) were found to bear sculpturing across more than three species. Sculpturing was found to extend beyond these seven bones onto either the dentary, surangular and/or quadrate within five species. Phylogenetic analysis showed that sculpturing evolved recently and repeatedly in several distinct lineages. The remaining 19 skull bones were smooth, except in the five species above, supporting the suggestion that smooth skull bones were ancestral in gekkotans. There is no apparent relationship between body size and the presence of bone sculpturing. The functional significance, if any, of sculpturing requires further investigation.

ADDITIONAL KEYWORDS: dermal ornamentation – microcomputed tomography – osteology.

INTRODUCTION

The elaboration of cranial skeletal elements is a widespread phenomenon among vertebrates, encompassing several discrete phenomena. Hypermorphosis has been proposed as a developmental process that promotes diversification of skull morphology (e.g. in frogs and toads; Paluh et al., 2020). Dermal ornamentation, often the result of hypermorphosis via hyperossification, can result in the formation of structures such as horns or casques (Rieppel, 1993), and is common (although sporadically distributed) across squamate reptiles. Bone sculpturing refers to variation in the surface texture (Romer, 1956; Coldiron, 1974; Witzmann, 2009; Daza et al., 2014; Fig. 1), which also can be due to hyperossification.

Bone sculpturing has been observed on the cranial elements of taxa spanning several vertebrate groups (Miles, 1967; de Ricqlès et al., 2001; Paluh et al., 2020), such as basal tetrapods (Bystrow, 1935; Schoch, 2002; Witzmann & Soler-Gijon, 2010; Janis et al., 2012; Rhinehart & Lucas, 2013; Morkovin, 2015) and crocodiles (de Buffrénil, 1982; de Buffrénil et al., 2011, 2016; Clarac et al., 2016, 2017). Previous studies have surveyed patterns of cranial sculpturing across a wide array of vertebrate taxa, noting intraspecific variation and identifying distinct developmental processes that may be responsible for the diversity of patterns seen among them (Clarac et al., 2016). Other studies have revealed that the phylogenetic signal of cranial sculpturing in basal tetrapods becomes more regular and pronounced as the lineage persists (Witzmann et al., 2010), and have hypothesized that sculpturing may be associated with physiological processes such

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as cutaneous respiration or thermoregulation by means of the rete vasculosum.

Regardless of functional implication or developmental processes, the broad surveys described above provide clear evidence of how large-scale patterns of phenotypic diversity in the sculpturing of cranial bones can exist across a vertebrate group. Some taxa exhibit bone sculpturing characterized by rugosities or pitted structures (e.g. temnospondyls and squamates; Witzmann et al., 2010; de Buffrénil et al., 2011; Paluh et al., 2020), whereas in other cases, sculpturing has been identified as being grooved (Zylberberg & Castanet, 1985). However, for many species bone sculpturing is completely absent, and all cranial elements are smooth (de Buffrénil et al., 2016).

Geckos (Gekkota) are one of the most species-rich major clades of lizards, with more than 1900 species currently divided into seven families: the eyelid geckos, Eublepharidae, with controversial affinities within Gekkota (Burbrink et al., 2020), and two well-supported clades, Pygopodoidea (Pygodidae, Carphodactylidae, Diplodactylidae) and Gekkonoidea (Sphaerodactylidae, Phyllodactylidae, Gekkonidae) (Gamble et al., 2012, 2015) and occupying most of the world between 30–40°N and 50°S (Meiri, 2020), including remote islands. Sculpturing is common in some squamate lineages (e.g. iguanians; Camp, 1923) and is nearly or completely absent in others (e.g. microteiids; Hernández Morales et al., 2020), and it has been previously stated that geckos are characterized by smooth cranial bones (Mateer, 1982; Lee et al., 2009; Conrad, 2008; Gauthier et al., 2012); however, the geckos sampled within these studies were scored as having smooth bones. Cranial bone sculpturing was recorded in geckos once a more diverse set of gekkotan skulls had been evaluated (Supporting Information, Table S1; Conrad, 2018) but, to date, a systematic characterization of these traits has not been conducted.

The goal of the present study was to systematically characterize variation in sculpturing in cranial bones across gekkotan species representing all seven families. Additionally, we also examine patterns of evolutionary transitions in these traits on a multigene molecular gekkotan phylogeny to elucidate trends in phenotypic diversification in bone sculpturing (Gamble et al., 2015).

**MATERIAL AND METHODS**

**VARIATION ACROSS ELEMENTS**

We examined skulls from adult individuals of 195 gekkotan species, representing 117 genera (Supporting Information, Appendix S1). Most specimens were represented as high-resolution X-ray micro-computed tomography images (CT scans); the remaining were skeletonized specimens, and digital photographs of skeletonized and cleared and stained specimens. Micro-CT tomographs were used to render 3D models...
using Avizo Lite 9.5.0 (© FEI SAS, Thermo Fisher Scientific, 2018). Skeletonized specimens were viewed using a Leica MZ6 dissecting microscope. For each specimen, variation of sculpturing was scored for each of the 26 bones comprising the skull (Fig. 5; Appendix S2). Each trait was treated as an unordered multi-state character, whose states were defined based on previous anatomical descriptions (Rieppel, 1984; Estes et al., 1988; Conrad, 2008; Evans, 2008; Gauthier et al., 2012). Character states were as follows: (0) bone smooth, (1) bone grooved or vermicular, (2) bone pitted or pitted and ridged, and (3) bone rugose or with projections (Fig. 2). Cranial bones not universally present in all gekkotan species (e.g. the lacrimal, parafrontals, supratemporals and/or osteoderms) were coded as being inapplicable (–) if absent from the skull. When species displayed osteoderms, they were dichotomously scored as being smooth (0) or bearing sculpture (1).

**Phylogenetic Variation of Sculpturing**

To characterize the evolutionary history of changes in sculpturing patterns of the bones across the phylogeny at the species level, we used a multi-locus, time-calibrated molecular phylogeny for Gekkota (Gamble et al., 2015). The phylogeny and our dataset were pruned to include only shared species, resulting in 113 species for which both evolutionary history and patterns of cranial sculpturing information were available. Using this phylogeny, evolutionary changes in sculpturing patterns across species were evaluated using ancestral state estimation. Using R (R Core Team, 2019), three different approaches were implemented for comparison: maximum parsimony, maximum likelihood (Pagel, 1999) and Bayesian stochastic character mapping (Huelsenbeck et al., 2003; Bollback, 2006). Maximum parsimony estimates were generated using the asr_max_parsimony function in the castor package (Louca & Doebeli, 2018). Similarly, maximum likelihood estimates for ancestral states were completed with the equal rates model across the phylogeny using the ace function from the ape package (Paradis et al., 2004). For Bayesian stochastic character mapping we generated 1000 stochastic maps using the equal rates model across the phylogeny using the phytools package (Revell, 2012). We then

![Figure 2](https://academic.oup.com/biolinnean/article-lookup/131/4/801/5924664)
summarized the resulting 1000 stochastic maps to obtain estimates of changes in cranial sculpturing characters. As maximum parsimony bases ancestral states on the minimum number of state changes along the phylogeny, branch length differences and unequal transition rates among character states were not considered. We therefore focused on the results from stochastic mapping.

**ONTGENETIC VARIATION**

To better understand the onset of bone surface sculpturing, we gathered additional CT data of two post-hatchling series from the most extensively sculptured species, *Chondrodaictylus bibronii* (Gekkonidae, pitted) and *Saltuarius salebrosus* (Carphodactylidae, rugose). Individuals were selected for the post-hatchling series based on snout–vent length (SVL).

**RESULTS**

**Variation across elements**

Skull surface sculpturing was identified in 28 genera across Gekkota, although the vast majority of bones in the skull were characterized as having smooth surfaces. All three sculpturing types (grooved, pitted, and rugose) previously identified in vertebrate taxa (e.g. squamates, crocodiles and temnospondyls: Zylberberg & Castanet, 1985; Witzmann & Soler-Gijon, 2010; Clarac et al., 2016) were seen in the Gekkota (Fig. 3). The grooved sculpture was found in 28 taxa (Carphodactylidae: *Nephurus levis*, *Underwoodisaurus miliii*; Diplodactylidae: *Bavayia montana*, *Bavayia sauvagii*, *Dactylocnemis pacificus*, *Hoplodactylus duvaucelii*, *Lucasium damaeum*; Eublepharidae: *Goniurosaurus araneus*, *Hemitheconyx caudicinctus*, *Hemitheconyx taylori*, *Holodactylus africanus*; Gekkonidae: *Blaesodactylus boivini*, *Chondrodaictylus anguiler*, *Gehyra marginata*, *Gehyra vorax*, *Gekko gecko*, *Gekko smithii*, *Hamadryas giganteus*, *Hamadryas mabouia*, *Hamadryas turcicus*, *Homopholis wahlbergii*, *Holodactylus phanastaticus*; Phyllodactylidae: *Haemodracon riebeckii*, *Phyllolepida anguiler*, *Thecadactylus rapicauda*; Sphaerodactylidae: *Quedenfeldtiia trachyblepharus*), pitted sculpture in two (Gekkonidae: *Blaesodactylus antongilensis* and *Chondrodaictylus bibronii*) and rugose sculpture in 11 (Carphodactylidae: *Carphodactylus laevis*, *Oraya occultus*, *Phyllurus platurus*, *Saltuarius salebrosus*; Diplodactylidae: *Naultinus grayii*, *Pseudothecadactylus australis*, *Pseudothecadactylus lindneri*, *Rhacodactylus leachianus*, *Rhacodactylus trachyrhynchus*; Gekkonidae: *Matoatoa breviceps*, *Paroedura stumpffi*). Furthermore, when sculpturing was present, it was not uniformly distributed across the bones of the skull, but rather was concentrated across the seven dermal roofing bones (Figs 4, 5). If sculpturing was present in the skull, it was always present on the frontal bone. Often if sculpturing was present it occurred in the midline (maxillae, nasals, prefrontals, frontal, parietals) and occurred more laterally either towards the snout region or towards the back of the cranium. Interestingly, in *Chondrodaictylus bibronii* the pitting sculpture was extended to the quadrate, an endochondral bone (Fig. 5). This extension of sculpture to the quadrate was also seen with rugose bones found in *Carphodactylus laevis* and *Saltuarius salebrosus*. Additionally, two cases of sculpturing were observed on the dentary and surangular in *Homopholis wahlbergi* and *Chondrodaictylus bibronii* (Fig. 4).

**Phylogenetic variation**

For this analysis, there were only seven bones (premaxilla, maxilla, nasal, prefrontal, frontal, parietal and postorbitofrontal) that expressed sculptural variation across three or more taxa. The remaining 19 bones were either invariant across all species (smooth), or the sculptured bone was only observed in one or two species. Ancestral states were estimated only for the seven bones that had sculptural variation for more than three species. Evaluating these patterns from an evolutionary perspective inferred smooth skull bones as the basal condition of the gekkotan ancestor. It also revealed that sculpturing evolved recently and repeatedly in several distinct lineages (Fig. 5). In this analysis, grooved bones were inferred to have evolved at least 13 times independently across six of the families within Gekkota. Grooved bones were implied to have evolved more frequently at branch tips, as seen with *Hamadryas turcicus*, *Chondrodaictylus anguiler*, *Uroplatus phanastaticus*, *Phyllolepida lutzai*, *Thecadactylus rapicauda*, *Haemodracon riebeckii* and *Underwoodisaurus miliii*. However, in one instance there was an ancestral estimation of grooved frontal and parietal bones for a clade within eublepharids (comprising *Hemitheconyx caudicinctus*, *Holodactylus africanus*, *Eublepharis macularius* and *Goniurosaurus araneus*, with a reversal to smooth bones in *Eublepharis macularius*). Pitted bones also were estimated on the tips as the single occurrence on cranial bones was noted for *Blaesodactylus antongilensis*. Rugose sculptured bones evolved at least twice in the pygopodoideans and once in the gekkonoidean genus *Matoatoa*. For the carphodactylids in this study, an ancestral state of a rugose sculpture was estimated for the frontal and parietal, as seen with the grooved sculpture, and...
for the node shared by *Pseudothecadactylus lindneri* and *Rhacodactylus leachianus* among diplodactylids. Furthermore, evolutionary transitions from the ancestral condition (smooth) to sculpturing were concentrated on particular branches of the phylogeny, implying that the evolution of sculpturing occurred simultaneously in multiple bones during gekkotan evolutionary history. Extant gekkotan species either exhibited the smooth condition for all bones of their skull, or displayed several sculptured bones, rather than bearing sculpturing on only one bone. In the two instances where the estimated ancestral state was not smooth, multiple skeletal elements were estimated as being primitively sculptured (Fig. 5). Finally, results from both maximum likelihood and Bayesian stochastic character mapping yielded identical patterns of inferred evolutionary changes in character states across the phylogeny (Fig. 5), and patterns inferred by maximum parsimony were largely concordant (Supporting Information, Fig. S1).

**Ontogenetic Variation**

Both *Chondrodactylus bibronii* (Gekkonidae, pitted) and *Saltuarius salebrosus* (Carphodactylidae, rugose) showed an incremental increase in the sculpturing of roofing bone elements with age. However, the sculpturing sequence observed between these two groups is slightly different.
Chondrodactylus bibronii

The skull of the youngest stage available for this species measured 15.12 mm, about twice the size of that of a hatchling, where the skull length was taken from the tip of the premaxilla to the occipital condyle. At this early stage all the roofing bone elements are sculptured, with the pitting appearing more scattered when compared to older individuals. However, some bones are sculptured toward the medial line and retain smooth peripheral surfaces, as seen with the marginal border of the maxilla or the dorsolateral surface of the postorbitofrontal bone. The sculpturing on the jaw is less extensive, being present on the posteroventral surface of the dentary, and mainly on the compound bone. Additionally, most of the suture seams are still visible. In the young adult (skull length 22.09 mm), the pitting is denser. Additional pitting appears at the base of the facial process of the maxilla, near the edge of the postorbitofrontal, yet, interestingly, the dentary remains primarily smooth. In the older adult (skull length 26.22 mm), the sculpturing is more densely packed, to the point that individual pits begin to merge, to create larger and deeper pits. Some bones that were not sculptured in the smaller specimens are pitted in the larger individual (e.g. the quadrate), and the pitting on the jaw extends further anteroventrally. Suture seams become diffuse, particularly in the snout; for example, the naso-frontal suture seam, and the maxillonasal sutures are nearly indistinguishable, indicating some degree of synostosis. In the older adult, all regions of the external surface except the labial regions and the areas of jaw muscle attachment are sculptured.

Saltuarius salebrosus

The skull of the youngest stage available of this species measured 19.87 mm, much larger than a hatchling of this species, as demonstrated by the fact that the parietal fontanelle is nearly obliterated. Although the skull of this juvenile specimen is larger than that of our smallest Chondrodactylus bibronii, in this species, the only sculpturing visible was a few bumps in the midline of the frontal and parietal. In the young adult (29.88 mm), the rugosities are more densely packed, extending along the tip of the facial process of the maxilla and over the entire surface of the nasals, prefrontal, frontal, parietals and postorbitofrontals.

Figure 4. Skull of Chondrodactylus bibronii showing the splanchnocranium in yellow, the chondrocranium in blue and the dermatocranium in red (A). Uniquely among geckos, this species exhibits sculpturing on a splanchnocranial element, the quadrate, here shown in anterior (B), lateral (C) and posterior (D) views.
At this stage, the rugosities display different degrees of development; the large rugosities are equidistant, and surrounded by smaller ones. In the older adult (37.68 mm), the rugosities have attained their maximum size, giving the roofing bones of the skull a spiky appearance, with additional rugosities being present on the nasal process of the premaxilla. Unlike *Chondrodactylus bibronii*, *Saltuarius salebrosus* does not develop sculpturing on the jaw or quadrate bones.

**DISCUSSION**

**VARIATION ACROSS ELEMENTS**

Gekkota displayed three sculpturing patterns on their cranial bones that have been previously identified in other taxa: grooved, pitted and rugose. The exception of three taxa, we found that when sculpturing was present, it was restricted to the dermal bones of geckos, as is seen across other osteichthyan...
taxa (Witzmann et al., 2010; de Buffrénil et al., 2016). Further work should focus on the developmental differences of Chondrodactylus bibronii, Saltuarius salebrosus and Carphodactylus laevis that leads to the sculpture on the endochondral bone, the quadrate. One unexpected finding of our study is that when osteoderms were present (as seen in Tarentola mauritanica, Gekko gecko and Geckolepis maculata), sculpturing patterns on the osteoderms that were observed did not correspond to those observed on the cranial bones. The osteoderms are smooth for Geckolepis maculata and pitted for Tarentola mauritanica, but in Gekko gecko they display both grooved and rugose characteristics (Laver et al., 2020). While this may represent a unique sculptural pattern in geckos, the present study cannot determine intraspecific variation because only a single adult specimen per species was examined. However, for each of these individuals the bones underlying the osteoderms were smooth.

**Phylogenetic Variation**

The estimated ancestral condition of geckos is to have a smooth skull, which explains why this trait has been mentioned before as a synapomorphy of the group; however, this trait seems to be symplesiomorphic for squamates in general (Gauthier et al., 2012). Non-ornamented bones are present in stem gekkotans, such as the Lower Cretaceous Norellius nyctisaurops (~130 Mya; Conrad & Norell, 2006; Conrad & Daza, 2015), Gobekko cretacicus (Borsuk-Bialynicka, 1990; Daza et al., 2013), and an unnamed form from the Mid-Cretaceous; these two named fossils have been recovered as consecutive sister taxa to Gekkota (~99 Mya; Daza et al., 2016). Another fossil taxon that is frequently recovered as closely related to gekkotans is Eichstaettisaurus schroederi, which also has unsculptured bones (Simões et al., 2017). Thus, based on optimization of this trait in available phylogenies, and outgroup comparisons, it can be stated that sculpturing on cranial bones in geckos is a derived trait and has evolved independently in several lineages on the gekkotan tree. Based on the phylogenetic distribution of sculpturing across gekkotan taxa, one can infer that sculpturing has evolved at least 18 times in the group (see Fig. 5). Several additional species within Gekkota are known to display cranial sculpturing (e.g. Nephrurus sheai, Rhacodactylus trachycephalus, Saltuarius swaini complex), but these are not represented in the most recent molecular phylogeny for the group (Gamble et al., 2015). However, none of these species is expected to represent additional independent instances of derivation of the trait.

The two families with the largest mean body sizes, the Carphodactylidae and Eublepharidae, display sculptured frontal and parietal bones as their ancestral condition. While these observations may suggest a degree of evolutionary allometry to bone sculpturing, where increased sculpturing is observed in larger species, patterns seen in other families, such as the Gekkonidae, are not consistent with this interpretation as bones appear to be sculptured at any body size (Supporting Information, Fig. S2). However, correlation between body size and cranial sculpturing should be directly addressed with future work. Additionally, Matoatoa breviceps, with a skull length of about 8 mm, displays rugose bone sculpturing and Quedenfeldtia trachyblepharis, with a skull length of about 11 mm, displays grooved bone sculpturing. Therefore, when the trait is viewed across Gekkota, there is no apparent relationship between the degree of bone sculpturing and skull size. Furthermore, when sculpturing was present, it was displayed concurrently across bones, as evidenced by the adjacent bones displaying evolutionary changes on the same branches of the phylogeny (Figs 4, 5). This indicates that a region of the dermis may be affected causing the change in these multiple intramembranous skeletal elements.

**Ontogenetic Variation**

Based on a small sample of the most highly sculptured species (Fig. 6), sculpturing appears to start in the middle of the roofing elements and extend ventrally towards the lateral edges of these bones. Relatively extensive sculpturing appears early in the gekkonid Chondrodactylus bibronii but is weakly developed in a young specimen of the carphodactylid Saltuarius salebrosus. Based on hatchling Nephrurus illustrated by Stephenson (1960), it is expected that hatchlings would exhibit entirely smooth skull surfaces. Skull variation during ontogeny is determined by the level of ossification from hatchling to adults (Evans, 2008); the increase in sculpturing through ontogeny is also a product of continued ossification, which not only affects the dermal bone surface, but also bone shape and density, and patterns of suturing between the roofing bones. The two species sampled, showing some differences in the onset of sculpturing, indicate that this morphology is heterochronous among gekkotans and is variable, even among closely related species. This latter statement is supported by observations on one specimen of Chondrodactylus angulifer in which the skull is not pitted but has grooved sculpturing instead (Fig. 3).

Interpretation of the pattern of distribution of sculpturing within gekkotans is not completely clear; however, it is linked to shared common ancestry.
within pygopodoideans, in which there is a clear trend towards increased rugose and grooved sculpturing, especially within carphodactylids, and to some extent in the diplodactylids, with a complete lack of sculpturing in the attenuate and limb-reduced pygopods. In the Gekkonoidea, smooth bones are generally retained, with intermittent sculpturing, and sometimes contrasting character states within the same genus (e.g. *Chondrodactylus*). Remarkably, the only gekkonoids with a rugose sculpturing comparable to that developed in some pygopodoideans are the Madagascan gekkonids in the genus *Matoatoa*. The ‘rugosities’ in this species are more knob-like, occasionally spiky, and are concentrated in the snout (Heinicke et al., 2014), representing a convergent character state with pygopodoideans. Additionally, in *Matoatoa* the sculpturing is known to be co-ossified with the skin (Nussbaum et al., 1998).

**Figure 6.** Dorsal (A, C) and lateral (B, D) post-hatchling developmental series of two sculpturing types: pitted and rugose. Skull length (apex of premaxilla to occipital condyle measured from dorsal view) is shown by black bars.
In frogs with heavily sculptured bones, co-ossification is relatively common (Trueb, 1970; Jared et al., 2005; Paluh et al., 2020), but this pattern of co-ossification is relatively rare among gekkotans, yet occurs more frequently in medium- and large-bodied genera [e.g. Chondrodactylus, Paroedura and Tarentola (Heinicke et al., 2014)]. We examined one specimen of the carphodactylid Phyllurus platurus, using CT data and diffusible iodine-based contrast-enhanced computed tomography (diceCT: Gignac et al., 2016) to determine if the skin is also co-ossified. Although the rugosities in the skull often coincide with keratinous structures in the integument (e.g. spinous tubercles), in this specimen there was not an inevitable correlation between the external and internal structures (Fig. 7). We conclude then that at least in this specific observation, there may be a partial correlation whereby the rugosities might serve to increase the size of tubercles. Further analysis is needed, including histological preparations, to determine the precise relationship between the integument and skull as the diceCT data were insufficient to visualize this relationship. However, the small size and seemingly random placement of these tubercles would appear to preclude their use in defence as compared with, for example, the cranial spines of cordylids (e.g. Stanley & Bates, 2014; Broeckhoven et al., 2018).

One application of the data gathered in this study is in the analysis of the gekkotan fossil record. For example, most Palaeogene gekkotans are known from isolated cranial elements (Daza et al., 2014; Bolet et al., 2015), many of which are sculptured [e.g. Laonogekko lefevrei (rugose), Rhodanogekko viretti (rugose), Cadurcogekko piveteaui (grooved)]. We have demonstrated that among living geckos there is a discrete pattern regarding the distribution of sculpturing, with the frontal and/or parietal almost inevitably exhibiting such surface features if they are present elsewhere on the skull. Thus, an isolated fossil maxilla with sculpturing would imply that the frontal, and perhaps other midline bones, would also have sculpturing present. Such relationships among sculptured elements could be helpful in associating disarticulated material or in the reconstruction of probable features in the absence of key elements.

Possession of surface features on skull bones might also be useful for estimating potential relationships, because dermal sculpturing is limited to certain groups (Fig. 5). For example, the fragmentary Palaeogene Laonogekko lefevrei exhibits a low and wide facial process of the maxilla, as well as dermal sculpturing, both features that are more common in Australo-Pacific pygopodoideans than in gekkonoidans (Bauer, 1990). This could suggest that pygopodoids were once far more geographically widespread than they are at present. However, the demonstrated independent derivation of sculpturing across the gekkotan phylogeny means that such an interpretation would necessarily be speculative, and to be conclusive, we need more complete materials from these taxa.

Geckos display a wide array of morphological variation in dermal sculpturing, which is an important contributor to structural diversity in the cranium as this implies that these traits are shared due to similar functions. In other taxa, bone

Figure 7. The association of epidermal tubercles and underlying bony conical projections in the gecko Phyllurus platurus (Carphodactylidae, MCZ R-130254), indicated by circles. Note that not all superficial tubercles are coincident with underlying rugosities.
sculpturing has been suggested to play roles in functions as diverse as thermoregulation (Seidel, 1979; Clarac et al., 2016) – for example, gland excretions; Jared et al., 2015) – visual signalling (Prötzel et al., 2018) and mechanical reinforcement (Romer, 1947; Trueb, 1993; Dias & Richter, 2002; Witzmann, 2009). However, to date no functional analysis of cranial sculpturing has been performed in geckos, leaving this an important question for future study.

ACKNOWLEDGEMENTS

We thank Jessie Maisano, Matt Colbert, and the UTCT facility for the multiple CT scans, and Susan E. Evans as well as an anonymous reviewer for help in development of this paper. We also want to thank Mark Hutchinson for sharing CT scans of Orraya occultus. This study was funded by National Science Foundation grants including DEB 1657656, and the Department of Biological Sciences at Sam Houston State University. A.M.B. was supported by the Gerald M. Lemole Endowed Chair funds through Villanova University. Additional thanks go to the Gecko Lab at Sam Houston State University for providing the space and materials for these investigations, as well as to Monte Thies and Sibyl Bucheli for additional assistance and guidance in the development of this project.

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

**Appendix S1.** Details of specimens examined.

**Appendix S2.** Details of characters and character states.

**Figure S1.** Cranial sculpturing characters mapped onto the multi-gene phylogenetic tree using parsimony. Data were generated using the castor package in R for each bone and subsequently combined. Colours indicate state change where smooth (0) is black, grooved (1) is red, pitted (2) is green and rugose (3) is blue. Numbers correspond to the bones listed at the top of the figure.

**Figure S2.** Relationship between log of skull lengths of taxa and degree of frontal bone sculpturing condition (0 = smooth, 1 = grooved, 2 = pitted, 3 = rugose) showing the relationship between sculpturing and skull length.

**Table S1.** Prior literature on cranial bone sculpturing of geckos.