

Sheddable armour: identification of osteoderms in the integument of *Geckolepis maculata* (Gekkota)

DANIEL J. PALUH^{1,2*}, AARON H. GRIFFING^{1,3} & AARON M. BAUER¹

¹Villanova University, Department of Biology, Villanova, PA 19085, USA; ²Department of Biology and Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA; ³Marquette University, Department of Biological Sciences, Milwaukee, WI 53233, USA

Abstract.—Osteoderms are bony deposits that form within the dermal layer of skin in vertebrates. Within geckos, osteoderms are uncommon, only described in *Gekko gecko* and the genus *Tarentola*. A previous report of osteoderms in the Afro-Malagasy gekkonid genus *Geckolepis* has been questioned due to the extreme skin fragility and regional integumentary loss within the group. We re-evaluated the integument anatomy of *Geckolepis maculata* using μ CT scanning, histology, and clearing and staining to verify the presence or absence of osteoderms and, if present, to characterise and compare their morphology to the osteoderms of *Gekko gecko* and *Tarentola*, as well as osteoderm diversity within squamates. Osteoderms were confirmed present in *Geckolepis maculata*; however, these osteoderms are compound, imbricating, squamous elements that are morphologically similar to the dermal ossifications observed in scincids and gerrhosaurids, while *G. gecko* and *Tarentola* possess plate-like and granular osteoderms. Our results suggest that osteoderms have independently evolved at least three times within the Gekkota and that epidermal anatomy may be a better predictor of osteoderm morphology than ancestral history. Further research is required to investigate the regenerative capability of *Geckolepis* osteoderms following skin autotomy.

Key words.—Dermal skeleton; dermal ossifications; computed tomography; fish-scale gecko; Gekkonidae; Madagascar.

INTRODUCTION

Osteoderms are bony deposits that form within the dermis of skin that are prevalent within tetrapods, irregularly occurring in phylogenetic distribution in anurans, non-avian archosaurs, turtles, mammals and lizards (Moss 1969; Hill 2005; Vickaryous & Sire 2009). These elements are highly variable in size, shape, distribution, and the amount of mineralised and unmineralised connective tissue present within and between species (Grant 1944; Hoffstetter 1962; Vickaryous & Sire 2009); however, osteoderms likely represent the manifestation of a plesiomorphic, latent capability of the dermis to ossify (Vickaryous & Hall 2008). Osteoderms are common within squamates (exclusive of Serpentes) and are present within anguids, cordylids, gekkotans, xantusiids, gerrhosaurids, xenosaurids, lacer-tids, scincids, helodermatids, shinisaurids, lanthanotids, varanids and iguanids (Camp 1923; McDowell & Bogert 1954; Gauthier 1982; de Queiroz 1985; Arnold 1989; Conrad 2008; Stanley *et al.* 2011, Vickaryous *et al.* 2015). Within the Gekkota, osteoderms are uncommon, having only been reported in the Asian gekkonid *Gekko gecko* (Cartier

*Corresponding author. Email: dpaluh@ufl.edu

1872; Daza *et al.* 2015; Vickaryous *et al.* 2015) and six species of the phyllodactylid genus *Tarentola* (Otto 1909; Levrat-Calivac 1986; Vickaryous *et al.* 2015).

Typical gekkotan dorsal scalation consists of plate-like, granulate and juxtaposed scales interspersed with tubercles (Bauer *et al.* 1989), whereas ventral scalation is more imbricate and is less heterogeneous (Maderson *et al.* 1978; Bauer *et al.* 1989). Members of the Afro-Malagasy gekkonid genus *Geckolepis* (fish-scale geckos) are partially characterised by strongly imbricate, “cycloid” scales (we here refer to scale shape and imbrication and do not imply any special similarity to the cycloid scales of actinopterygian fishes; Werner 1896; Köhler *et al.* 2009). Within the Gekkota, only *Teratoscincus*, a West Asian sphaerodactylid, exhibits similar scalation (Werner 1896; Hiller 1974; Szczerbak & Golubev 1986; Bauer *et al.* 1993), although somewhat similar scales are found restricted to the tail of a few other species. As a complement to caudal autotomy, the integument of *Geckolepis* is highly fragile and utilised as a predator escape mechanism (integumentary autotomy or regional integumentary loss; Schmidt 1911; Angel 1942; Mertens 1955; Anderson 1972; Meier 1980; Schubert & Christophers 1985; Bauer & Russell 1992; Gardner & Jasper 2015). Schmidt (1911, 1912) provided a detailed histological description of *G. polylepis* dermis from across the body, comprised of a thin inner layer, a cell-poor loose connective tissue layer, and a thick outer layer with small, irregular osteoderms embedded within it (reviewed in Bauer *et al.* 1993). These osteoderms are described as being absent until late in ontogeny and form as separate small tiles that grow and aggregate during development. Schmidt’s reports have been questioned, however. Bauer & Russell (1989) suggested that the osteoderms Schmidt described were regional keratinisations rather than osteoderms. Additionally, Vickaryous *et al.* (2015) questioned the reports of Schmidt, in part because *Geckolepis* species are known to demonstrate regional integumentary loss, during which the outer layers of the integument are lost (Schubert & Christophers 1985; Bauer *et al.* 1989; Bauer & Russell 1992). Skin fragility can facilitate escape from a putative predator (Bauer *et al.* 1989; Gardner & Jasper 2015); however, easily shedding osteoderms would represent a loss of energy invested in their original development and an implied cost for subsequent regeneration. Further, osteoderms and fragile skin would appear to reflect conflicting strategies for defence.

We investigated *Geckolepis* integument anatomy using micro-computed tomography, histology, and clearing and staining. We compare *Geckolepis* to other gekkotan taxa known to have osteoderms (*Gekko* and *Tarentola*), as well as *Teratoscincus*, the only other gekkotan known to have bodywide large, imbricate, cycloid scales. Our goals are to determine if osteoderms are present or absent in *Geckolepis* and, if present, to characterise and compare their morphology to osteoderm diversity within squamates.

Table 1. Snout-vent length and micro-computed tomography settings for specimens examined in this study.

Species	Collection number	SVL (mm)	Current (kV)	Amperage (μ A)	Watts (W)	Acquisition time (s)	Voxel (μ m)
<i>G. maculata</i>	CAS 126344	51	70	143	10	2	18
<i>G. gecko</i>	SHSVM-H-0001-2014	161	200	240	48	2	44
<i>G. smithii</i>	CAS 9595	175	79	143	10	2	36
<i>T. mauritanica</i>	CAS 87112	50	70	143	10	2	18
<i>T. przewalskii</i>	CAS 171013	91	n/a	n/a	n/a	n/a	21

METHODS

The heads of an adult *Gekko gekko* (SHSVM-H-0001-2014), *Tarentola mauritanica* (CAS 87112), *Geckolepis maculata* (CAS 126344), *Gekko smithii* (CAS 9595) and *Teratoscincus przewalskii* (CAS 171013) were computed tomography (CT) scanned using an Xradia MicroCT scanner (Pleasanton, CA, USA) at the University of Texas High-Resolution X-ray Computed Tomography Facility (see Table 1 for CT settings). Visualisation and measurements of the 2-dimensional tomograms and 3-dimensional volume renderings were completed using Avizo 9.0.1 (VSG, Visualisation Sciences Group, Burlington,

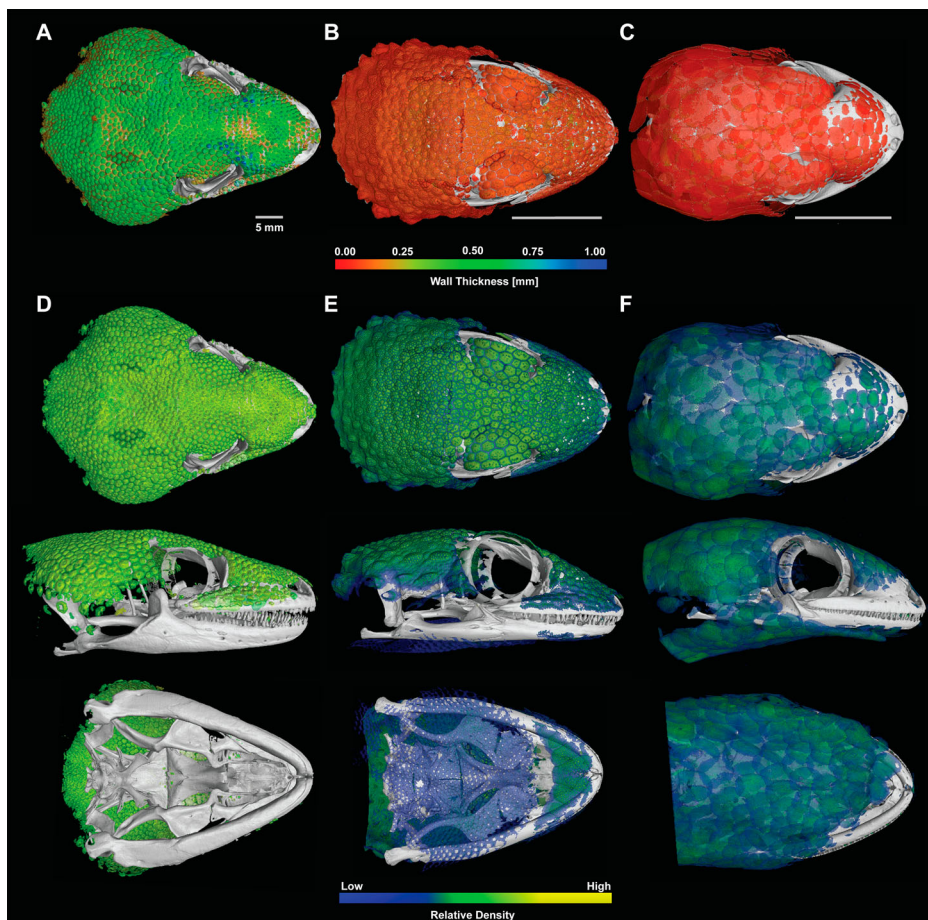


Figure 1. Computed tomography (CT) reconstruction of the skull and osteoderms of (A, D) *Gekko gekko* (SHSVM-H-0001-2014), (B, E) *Tarentola mauritanica* (CAS 171013) and (C, F) *Geckolepis maculata* (CAS 126344). (A–C) Cross-sectional thickness of osteoderms measured using a wall-thickness analysis and visualised using an inverse rainbow colour gradient on a standardised scale ranging from 0.00 to 1.00 mm thickness. (D–F) Relative density of osteoderms measured using grey-scale histogram values (calibrated to the same scale by standardising the void [as background] and skeletal bone [as material] for all specimens) and colour-coded using an interval gradient rendering high density material yellow and low density material blue in dorsal, lateral and ventral view (top to bottom, respectively). Scale bar = 5 mm.

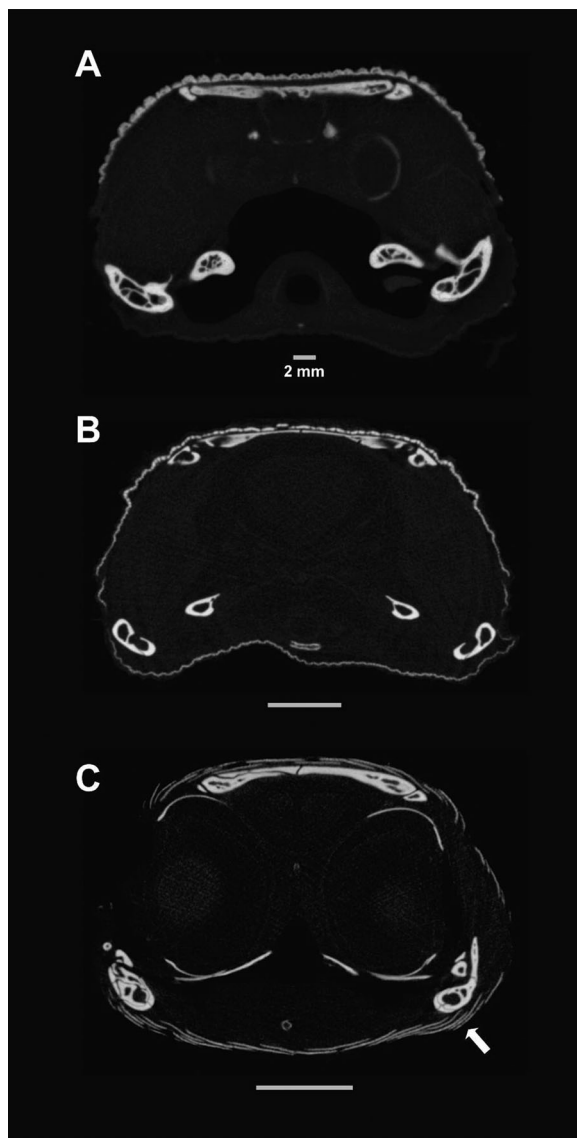


Figure 2. Transverse cross section tomogram of (A) *Gekko gecko* (SHSVM-H-0001-2014), (B) *Tarentola mauritanica* (CAS 126344) and (C) *Geckolepis maculata* (CAS 126344). All cross sections are from the parietal-frontal suture point of the skull. Imbricating osteoderms are present within *Geckolepis maculata* (white arrow). Scale bar = 2 mm.

MA, USA) and VGStudio Max 3.0 (Volume Graphics, Heidelberg, Germany). The cross-sectional thickness of the segmented osteoderms were measured using the wall-thickness analysis module in VGStudio Max and visualised using an inverse rainbow colour gradient on a standardised scale (ranging from 0.00 to 1.00 mm thickness; Fig. 1A–C). The greyscale histograms of the tomograms were calibrated to the same scale for all specimens in VGStudio Max by standardising the grey values of the background (void) and material of interest (dermal bone), and the relative density of the segmented

osteoderms were measured and visualised at every voxel using a colour interval gradient, rendering high density material yellow and low density material blue (Fig. 1D–F). Transverse cross sections of the X-ray tomograms were examined at the parietal-frontal suture point of the skull for all taxa (Fig. 2), as osteoderms in gekkotans, and most other lizards, are typically robust in this region. Three dimensional stereolithography (STL) shape data are available to view and download from Duke University’s morphological data archive (http://morphosource.org/Detail/ProjectDetail/Show/project_id/318).

Additionally, an adult *Geckolepis maculata* specimen (UMMZ 207363; 67 mm snout to vent length (SVL)) was used for histological cross sectioning and clearing and staining of the integument. Scales of *G. maculata* were compared with a commercially obtained adult *Teratoscincus keyserlingii* (AMB 9211; 91 mm SVL). Excised patches of integument were removed from the dorsum of the trunk (scapular region) and head (parietal region) of *G. maculata* and the dorsum of the trunk of *T. keyserlingii*. Scales of both *G. maculata* and *T. keyserlingii* were decalcified for 15 hours in Formical-2000™ (Decal Chemical Corp, Tallman, New York, USA), dehydrated and embedded in paraffin wax to investigate their histological composition. Using a rotary microtome, transverse sections of isolated scales were cut at 6 µm thickness and subsequently affixed onto slides (following decalcification and dehydration, the excised patches of integument divided into isolated scales). Sections were stained with Masson’s trichrome (modified from Humason 1979 and Garvey 1984; Griffing 2016). Following the methodology of Vickaryous *et al.* (2015), we cleared and stained excised patches of skin containing multiple scales with Alizarin red to identify the presence or absence of mineralised tissue within the dermis (osteoderms) and subsequently characterised their pattern and shape within the integument using light microscopy.

RESULTS

Computed Tomography

Osteoderms were identified in CT scans of three gekkotan taxa, *Gekko gecko* (Fig. 1A, D), *Tarentola mauritanica* (Fig. 1B, E) and *Geckolepis maculata* (Fig. 1C, F), but were absent in *Gekko smithii* and *Teratoscincus przewalskii* (Fig. 2). The average cross-sectional thickness of osteoderms in the *G. gecko* specimen examined is 0.6 mm (Fig. 1A), which is much greater than the average cross-section thickness of osteoderms in the *T. mauritanica* and *G. maculata* specimens (<0.1 mm; Fig. 1B and C, respectively). The disparity in osteoderm thickness may be explained by the much larger body size of *Gekko gecko* (Table 1). The osteoderms of *G. gecko* and *T. mauritanica* have been previously described in detail (Vickaryous *et al.* 2015), and our CT reconstructions are consistent with these descriptions in that the osteoderms on the dorsum of the head range from plate-like to granular elements. The plates that develop from separate centres of ossification are heavily fused and very dense in *G. gecko*, whereas the osteoderms in *T. mauritanica* are unfused and lower in volumetric density. The osteoderms in the frontal and supraorbital region of *T. mauritanica* are enlarged plates in comparison to the remainder of the head and these are the first osteodermal elements to appear in the ontogeny of this species (Vickaryous *et al.* 2015). The osteoderms overlie the entire dorsum of the head in both species, become less dense laterally, and are absent on the venter of the head of *G. gecko* and are present in very low volumetric density on the venter of the head of *T. mauritanica*. The unfused osteoderms of *T. mauritanica* are relatively flat in cross section (Fig. 2B), while

the densely interlocking osteoderms of *G. gecko* are knob-like and form a rugose surface (Fig. 2A), resembling the beaded osteoderms of *Heloderma* (Vickaryous & Sire 2009). *Gekko smithii* exhibits no evidence of osteoderms, as documented by Vickaryous *et al.* (2015) using cleared and stained specimens. *Teratoscincus przewalskii*, a representative of the only other gekkotan genus known to possess bodywide cycloid scales, also lacks osteoderms, but is one of the two gecko genera to possess parafrenal bones in the supraorbital region of the eye (Bauer & Russell 1989; Griffing 2016).

The osteoderms of *Geckolepis maculata* are lower in volumetric density than in both *G. gecko* and *T. mauritanica*, as illustrated by the density gradient (Fig. 1D–F). Unlike the plates and granules in *G. gecko* and *T. mauritanica*, the entirety of each cycloid scale appears to be ossified—although at a differential density within and between individual scales (but see Histology and Clearing and Staining results). The centre of each scale is generally densest, while the periphery, which overlaps and is overlapped by other scales, is less dense. The osteoderms of *G. maculata* are on the dorsum, lateral surface and venter of the head in similar distribution and relative densities, however, the labial scales appear to

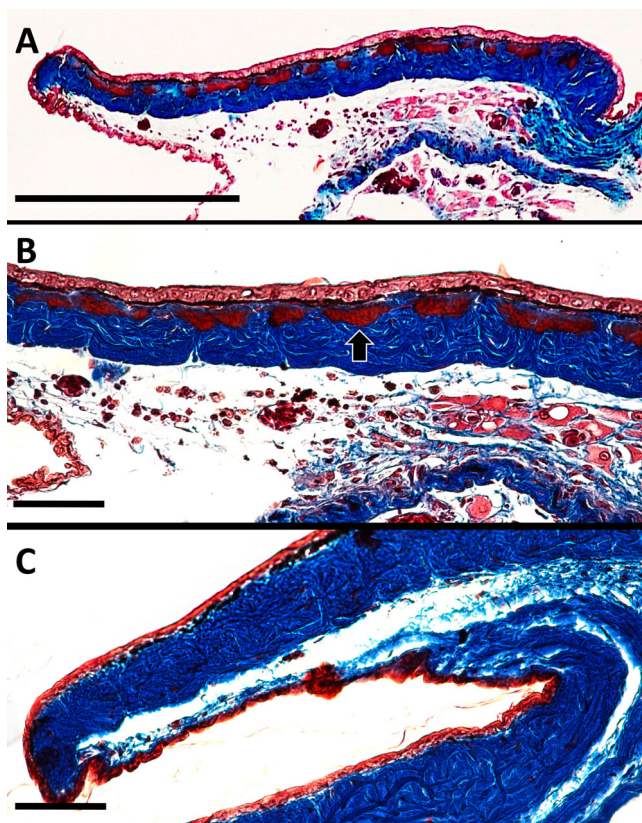


Figure 3. Sagittal section through a dorsal scale of *Geckolepis maculata* (UMMZ 207363) and *Teratoscincus keyserlingii* (AMB 9211). (A) 40× magnification of an entire *G. maculata* scale, scale bar = 500 μm; (B) 200× magnification of anterior portion of *G. maculata* scale. Osteoderms are embedded within the dermis (black arrow), scale bar = 50 μm; (C) 200× magnification of *T. keyserlingii* scale. Dermis is comprised of a thick, collagenous layer without osteoderms, scale bar = 50 μm.

contain no ossifications. The transverse cross section of *G. maculata* illustrates the heavily imbricate osteoderms (Fig. 2C), in contrast to the non-overlapping osteoderms of *G. gecko* and *T. mauritanica* (Fig. 2A,B).

Histology

Osteoderms were confirmed to be present in both the head and trunk scales of *Geckolepis maculata* through histology (Fig. 3A,B), whereas no osteoderms were present in the cycloid scales of *Teratoscincus keyserlingii* (Fig. 3C). Osteoderms of *G. maculata* are distributed throughout the length of the scale excluding the tip and base (Fig. 3A), embedded directly beneath the epidermis and within the stratum superficiale of the dermis. No stratum laxum is present within the dermis, and there is poor differentiation between the stratum compactum and stratum superficiale. Small gaps, ranging from 5–15 μm in length, are present between the individual plates. The osteoderms do not co-ossify with underlying dermal bones. The elements themselves are irregular in shape and very thin (approximately 8–14 μm thick; Fig. 3B), unlike the robust, block and sphere-like osteoderms exhibited in histosections of *G. gecko* and *Tarentola* (Bauer & Russell 1989; Vickaryous *et al.* 2015). We were unable to determine if osteodermine, a capping layer of enamel-like tissue (de Buffr enil *et al.* 2011, Vickaryous *et al.* 2015), is present within *Geckolepis maculata*.

Clearing and Staining

Osteoderms were confirmed present in the cleared and stained head and trunk scales of *Geckolepis maculata*. The scales were Alizarin red-positive (Fig. 4A), indicating the

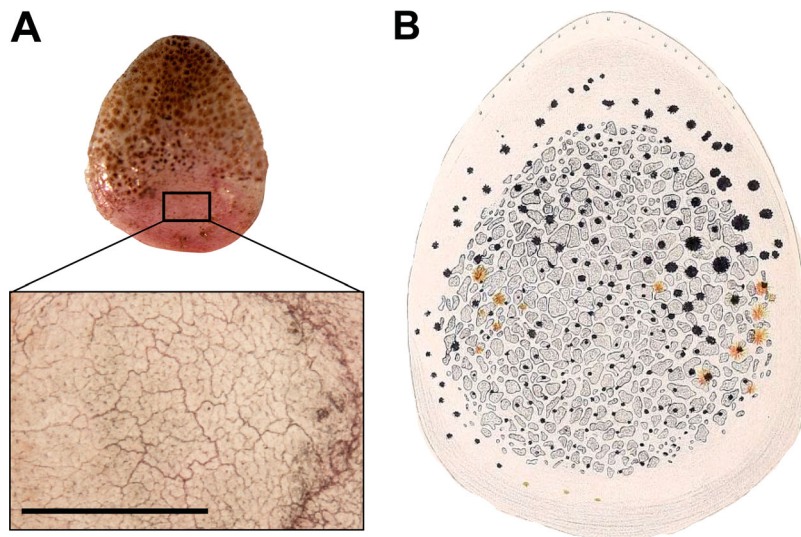


Figure 4. (A) Cleared and stained cycloid scale and osteoderms of *Geckolepis maculata* (UMMZ 207363). Inset is 100 \times magnification of cycloid scale illustrating highly interlocking osteoderm tesserae. Scale bar = 500 μm . (B) Reproduction of *Geckolepis polyepes* cycloid scale and osteoderms from the dorsum of the trunk (from Schmidt 1911).

presence of mineralisation, while the scales of *Teratoscincus keyserlingii* were Alizarin red-negative. Removal of the epidermis revealed the presence of very small, interlocking osteoderms that are expressed across the length and breadth of each scale excluding the peripheral edge (Fig. 4A), similar in morphology to the description and illustrations of Schmidt (1911; Fig. 4B). Many centres of ossification are present and the polygon-shaped elements directly abut one another, and in some cases fuse, forming a large plate of tightly interlocking tesserae that corresponds in overall shape to the epidermal scale.

DISCUSSION

Our μ CT and histological investigation confirm the presence of osteoderms within the integument of *Geckolepis maculata*, as earlier proposed by Schmidt (1911), therefore resolving a longstanding controversy. The osteoderm plates appear to be tightly interlocking tesserae (Fig. 4A), although they seemingly develop as small individual elements (Fig. 3), and aggregate during ontogeny to cover the length and breadth of each scale excluding the peripheral edge (Fig. 1C, F). Our histological cross-sections of *Geckolepis* osteoderms illustrate gaps between the mineralised plates and are likely at an earlier stage of maturation, while the resolution of our μ CT data is too low to identify the fine-scale structure of the interlocking tesserae. There may be variation in the degree of osteoderm fusion across the body of *Geckolepis*, but this is unassessed in this study. We also verify and describe the osteoderms of *G. gecko* and *T. mauritanica*, further demonstrating the utility of μ CT for visualising and quantifying squamate osteoderms (Maisano *et al.* 2002; Bever *et al.* 2005; Greenbaum *et al.* 2012; Stanley *et al.* 2016). The three osteoderm-bearing gekkotan taxa investigated in this study are distantly related (*Geckolepis maculata* and *Gekko gecko* are within Gekkonidae and *T. mauritanica* is within Phyllodactylidae; Gamble *et al.* 2015), therefore suggesting that osteoderms have independently evolved at least three times within Gekkota. The disparate osteoderm morphology between the two gekkonid taxa further supports this hypothesis. Although our study only assessed head osteoderm morphology in detail, Schmidt (1911, 1912) reported the presence of osteoderms across the entire body, and Scherz *et al.* (2017) have identified osteodermal elements that extend the whole body circumference in other species of *Geckolepis* using μ CT (see Figure 5 in the online [supplemental data](#)).

Previous work has questioned Schmidt's reports of osteoderms within *Geckolepis* due to the extreme skin fragility within the genus (Angel 1942; Vickaryous *et al.* 2015); however, Sensale *et al.* (2014) recently predicted that lepidosaurian osteoderm growth and development is less energy demanding than in synapsids and archosaurs. Furthermore, the osteoderms of *Geckolepis* are very small and of low volumetric density, and we suggest that osteoderm regeneration succeeding skin autotomy may be more energetically feasible in *Geckolepis* compared to taxa that are heavily-armoured. Vickaryous *et al.* (2015) confirmed that at least some species of *Tarentola* have the ability to regenerate caudal osteoderms following tail autotomy, although the distribution and shape of the regenerated osteoderms differ from the original, coinciding with other morphological modifications in the regenerated tail (Bellairs & Bryant 1985), such as non-tubercular scalation. Interestingly, the regenerated osteoderms of *Tarentola* are more similar in morphology to the flat, thin osteoderms observed in our histological sections of *G. maculata* than the original, spherical osteoderms of *Tarentola* (Vickaryous *et al.* 2015). The presence of osteoderms and fragile skin appear to reflect conflicting strategies for defence; therefore, it may be

possible that osteoderms in *Geckolepis* do not function as armour. Alternatively, *Geckolepis* osteoderms may function as thermoregulation structures or deposits of labile calcium for eggshell formation, as has been proposed for archosaur osteoderms (Seidel 1979; Dacke *et al.* 2015).

Squamate osteoderm morphology is highly variable, including a vermiform form in varanids (McDowell & Bogert 1954; Erickson *et al.* 2003), a flat, imbricating, squamous form in anguids, scincids and cordyliforms (Camp 1923; Zylberberg & Castanet 1985; Levrat-Calviac *et al.* 1986; Estes *et al.* 1988; Zylberberg *et al.* 1992; Gauthier *et al.* 2012), and a non-imbricating granule, plate or bead-like form in xenosaurids, lanthanotids, shinisaurids and helodermatids (Camp 1923; Gao & Norell 2000; Maisano *et al.* 2002; Bever *et al.* 2005; Conrad 2008; Gauthier *et al.* 2012). The osteoderms of the anguid, *Anniella* is morphologically distinct, as each plate possesses branching, finger-like processes (Bhullar & Bell 2008). Squamous osteoderms can be further categorised as either compound, possessing many centres of ossification forming an interlocking plate (observed in scincids and gerrhosaurids; Camp 1923; Estes *et al.* 1988; Richter 1994), or simple, possessing a single centre of ossification (observed in anguids and cordylids; Zylberberg & Castanet 1985; Zylberberg *et al.* 1992; Krause *et al.* 2003). *Gekko gekko* and *Tarentola* spp. have been previously described to possess plate-like and granular osteoderms, but the osteoderms of *Geckolepis maculata* are morphologically similar to the imbricating, squamous form observed in scincids and cordyliforms. The *G. maculata* osteoderms are tightly interlocking tesserae and therefore form a compound plate; however, the individual tesserae are extremely small in comparison to the individual elements observed in scincids or gerrhosaurids. The osteoderm plate morphology of minute tightly interlocking tesserae is somewhat similar in morphology to caecilian dermal ossifications (Zylberberg & Wake 1990). Osteoderm morphology has been previously used as a taxonomically informative character (Camp 1923; Estes *et al.* 1988; Read 1986; Conrad 2008; Gauthier *et al.* 2012), but the disparity between gekkotans in the presence or absence of osteoderms (Vickaryous *et al.* 2015) and overall form (this study) suggests that osteoderm morphology is homoplastic and an unreliable taxonomic character. The scalation disparity between *Gekko gekko* and *Tarentola* (small, juxtaposed, granular scales interspersed with tubercles) versus *Geckolepis* (imbricating cycloid scales) suggests that epidermal anatomy and osteoderm morphology are more tightly correlated than osteoderm morphology and ancestral history.

Schubert & Christophers (1985) and Schubert *et al.* (1990) proposed that regional integumentary loss in *Geckolepis* is promoted by a pre-formed zone of splitting that exists beneath the skin, between the entirety of the integument and an underlying layer of connective tissue and subcutaneous fat tissue. These authors further suggested that a network of myofibroblasts exist within the zone of splitting that actively initiates integumentary autotomy. These reports were questioned by Bauer *et al.* (1989) and Bauer & Russell (1992), as other gekkotans that perform regional integumentary loss possess a pre-formed zone of weakness within the outer layer of the dermis and experience integumentary loss intradermally, rather than subdermally. Although not examined in this study (the fragility of *Geckolepis* integument prevented the histological sectioning of a complete patch of skin, therefore we examined isolated scales), we expect the architecture and mechanism of integumentary loss in *Geckolepis* to be largely consistent with those previously identified across a phylogenetically diverse sample of geckos (Bauer *et al.* 1989, 1992, 1993; Bauer & Russell 1992); however, further research is required.

We were unable to confirm the presence of osteoblasts or osteocytes within the histological sections of *Geckolepis maculata*. Schmidt (1911) also failed to identify osteoblasts and suggested these mineralizations may be formed from calcified tissue. Vickaryous and Hall (2008) similarly demonstrated that osteoderms develop within alligators in the absence of osteoblast cells, osteoid, and periosteum, but rather develops “via the direct transformation of the preexisting dense irregular connective tissue.” Osteoderms have been demonstrated to be highly variable in histological structure and process of development (Vickaryous & Hall, 2008; Vickaryous & Sire 2009); therefore, we reason that the position within the dermis and composition of mineralized tissue demonstrates that these elements within *Geckolepis maculata* are osteoderms. Our results suggest that osteoderms have independently evolved at least three times within Gekkota, and two lineages possess plate-like and granular osteoderms (*Gekko gecko* and *Tarentola*), whereas *G. maculata* possesses an imbricating, squamous osteoderm morphology similar to that of scincids and cordyliforms. Future research directions include investigating the formation and ontogeny of *Geckolepis* osteoderms, determining the distribution and density of *Geckolepis* osteoderms across the venter of the trunk, the limbs and tail, verifying the skin-loss mechanism in *Geckolepis*, and examining the regeneration capability of *Geckolepis* osteoderms following skin autotomy.

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SUPPLEMENTAL DATA

Supplemental data for this article can be accessed at <http://dx.doi.org/10.1080/21564574.2017.1281172>

REFERENCES

- ANDERSON, S.C. 1972. Adaptation in geckos. *Pac. Discovery* 25: 1–11.
- ANGEL, F. 1942. Les Lézards de Madagascar. *Mém. Acad. Malagache*. 36: 1–193.
- ARNOLD, E.N. 1989. Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. *Bull. Br. Mus. Nat. Hist. (Zool.)* 55: 209–257.

- BAUER, A.M. & A.P. RUSSELL 1989. Supraorbital ossifications in geckos (Reptilia: Gekkonidae). *Can. J. Zool.* 67: 678–684.
- BAUER, A.M. & A.P. RUSSELL 1992. The evolutionary significance of regional integumentary loss in island geckos: a complement to caudal autotomy. *Ethol. Ecol. Evol.* 4: 343–358.
- BAUER, A.M., A.P. RUSSELL & R.E. SHADWICK 1989. Mechanical properties and morphological correlates of fragile skin in gekkonid lizards. *J. Exp. Biol.* 145: 79–102.
- BAUER, A.M., A.P. RUSSELL & R.E. SHADWICK 1992. Skin mechanics and morphology in *Sphaerodactylus roosevelti* (Reptilia: Gekkonidae). *Herpetologica* 48: 124–133.
- BAUER, A.M., A.P. RUSSELL & R.E. SHADWICK 1993. Skin mechanics and morphology of the gecko *Teratoscincus scincus*. *Amphibia-Reptilia* 14: 321–331.
- BELLAIRS, A.D'A. & V. BRYANT 1985. Autotomy and regeneration in reptiles. In C. GANS & F. BILLET (Eds), *Biology of the Reptilia*. Vol. 15. Development B. John Wiley & Sons, New York: pp. 301–410.
- BEVER, G.S., C.J. BELL & J.A. MAISANO 2005. The ossified braincase and cephalic osteoderms of *Shinisaurus crocodilurus* (Squamata, Shinisauridae). *Paleontol. Electron.* 8: 4A.
- BHULLAR, B.-A.S. & C.J. BELL 2008. Osteoderms of the California legless lizard *Anniella* (Squamata: Anguillidae) and their relevance for consideration of miniaturization. *Copeia* 2008: 785–793.
- CAMP, C.L. 1923. Classification of the lizards. *Bull. Am. Mus. Nat. Hist.* 48: 289–481.
- CARTIER, O. 1872. Studien über den feineren Bau der Epidermis bei den Geckotiden. *Verh. Wurzburg. Physiol.-Med. Ges. N.F.* 3: 83–96, 2 pls.
- CONRAD, J.L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bull. Am. Mus. Nat. Hist.* 310: 1–182.
- DACKE, C.G., R.M. ELSEY, T. TROSCLAIR III, P.L., SUGIYAMA, J.G. NEVAREZ & M.H. SCHWEITZER 2015. Alligator osteoderms as a source of labile calcium for eggshell formation. *Journal of Zoology* 297: 255–264.
- DAZA, J.D., A.A. MAPPS, P.J. LEWIS, M.L. THIES & A.M. BAUER 2015. Peramorphic traits in the tokay gecko skull. *J. Morphol.* 276: 915–928.
- DE BUFFRÉNIL, V., J.-C. DAUPHIN Y., RAGE & J.Y. SIRE 2011. An enamel-like tissue, osteodermine, on the osteoderms of a fossil anguid (Glyptosaurinae) lizard. *Comptes Rendus Palevol* 10: 427–437.
- DE QUEIROZ, K. 1987. Phylogenetic systematics of iguanian lizards: a comparative osteological study. *Univ. Calif. Publ. Zool.* 118: 1–203.
- ERICKSON, G.M., A. DE RICOLES, V. DE BUFFRÉNIL, R.E. MOLNAR & M.L. BAYLESS 2003. Vermiform bones and the evolution of gigantism in *Megalania* – how a reptilian fox became a lion. *J. Vert. Paleontol.* 23: 966–970.
- ESTES, R., K. DE QUEIROZ & J.A. GAUTHIER 1988. Phylogenetic relationships within Squamata. In R. Estes & G. Pregill (Eds), *Phylogenetic Relationships of the Lizard Families*. Essays commemorating Charles L. Camp. Stanford University Press, Stanford, CA: pp. 119–281.
- GAMBLE, T., E. GREENBAUM, T.R. JACKMAN & A.M. BAUER 2015. Into the light: diurnality has evolved multiple times in geckos. *Biol. J. Linn. Soc.* 115: 896–910.
- GAO, K. & M.A. NORELL 2000. Taxonomic composition and systematics of late Cretaceous lizard assemblages from Ukhaa Tolgod and adjacent localities, Mongolian Gobi Desert. *Bull. Am. Mus. Nat. Hist.* 249: 1–118.
- GARDNER, C. & L. JASPER 2015. A fish-scaled gecko (*Geckolepis* sp.) escapes predation by a velvet gecko (*Blaesodactylus* sp.) through skin shedding. *Herpetol. Notes* 8: 479–481.
- GARVEY, W. 1984. Modified elastic tissue-masson trichrome stain. *Stain Technol.* 59: 213–216.
- GAUTHIER, J.A. 1982. Fossil xenosaurid and anguid lizards from the early Eocene Wasatch Formation, southeast Wyoming, and a revision of the Anguioidea. *Contributions to Geol., U. Wyoming* 21: 7–54.
- GAUTHIER, J.A., M. KEARNEY, J.A. MAISANO, O. RIEPPEL & D.B. BEHLKE 2012. Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. *Bull. Peabody Mus. Nat. Hist.* 53: 3–308.
- GRANT, C. 1944. Scale structure in Jamaican lizards of the genus *Celestus*. *Copeia* 1944: 109–111.
- GREENBAUM, E., E.L. STANLEY, C. KUSAMBA, W.M. MONINGA, S.R. GOLDBERG & C.R. BURSEY 2012. A new species of *Cordylus* (Squamata: Cordylidae) from the Marungu Plateau of south-eastern Democratic Republic of the Congo. *Afr. J. Herpetol.* 61: 14–39.
- GRIFFING, A.H. 2016. Developmental osteology of parafrontal bones in *Aristelliger* and *Teratoscincus* (Squamata: Sphaerodactylidae). MSc thesis, Villanova University, Villanova, PA, USA.

- HILL, R.V. 2005. Integrative morphological data sets for phylogenetic analysis of Amniota: the importance of integumentary characters and increased taxonomic sampling. *Syst. Biol.* 54: 530–547.
- HILLER, U. 1974. Morphology and function of the dorsal sound producing scales in the tail of *Teratoscincus scincus* (Reptilia: Gekkonidae). *J. Morphol.* 144: 119–130.
- HOFFSTETTER, R. 1962. Observations sur les ostéodermes et la classification des anguïdés actuels et fossiles (Reptilia, Sauria). *Bull. Mus. Natl. Hist. Nat.* 34: 149–157.
- HUMASON, G.L. 1979. *Animal Tissue Techniques*, 4th edn. W.H. Freeman and Co., San Francisco, CA.
- KÖHLER, G., H-H. DIERTHER, R.A. NUSSBAUM & C.J. RAXWORTHY 2009. A revision of the fish scale geckos, Genus *Geckolepis* Grandidier (Squamata, Gekkonidae) from Madagascar and the Comoros. *Herpetologica* 65: 419–435.
- KRAUSE, D.W., S.E. EVANS & K.-Q. GAO 2003. First definitive record of Mesozoic lizards from Madagascar. *J. Vert. Paleontol.* 23: 842–856.
- LEVRAT-CALIVAC, V. 1986. Étude comparée des ostéodermes de *Tarentola mauritanica* et de *T. neglecta* (Gekkonidae, Squamata). *Arch. Anat. Micr. Morphol. Expér.* 75: 29–43.
- LEVRAT-CALIVAC V., J. CASTANET & L. ZYLBERBERG. 1986. The structure of the osteoderms in two lizards: *Tarentola mauritanica* and *Anguis fragilis*. In: Z. ROČEK (Ed.), *Studies in Herpetology*. Charles University, Prague, pp. 341–344.
- MCDOWELL, S.B. & C.M. BOGERT 1954. The systematic position of *Lanthanotus* and the affinities of the anguimorph lizard. *Bull. Am. Mus. Nat. Hist.* 105: 1–42.
- MADERSON, P.F.A., S. BARANOWITZ & S.I. ROTH 1978. A histological study of the long-term response to trauma of squamate integument. *J. Morphol.* 157: 121–136.
- MAISANO, J.A., C.J. BELL, J.A. GAUTHIER & T. ROWE 2002. The osteoderms and palpebral in *Lanthanotus borneensis* (Squamata: Anguimorpha). *J. Herpetol.* 36: 678–682.
- MEIER, H. 1980. *Geckolepis*, eine besondere Gecko-Gattung Madagaskars. *Herpetofauna* 2(5): 11–14.
- MERTENS, R. 1955. Studien ber die Reptilienfauna Madagaskars. I. Beobachtungen an einigen madagassischen Reptilien in Leben. *Zool. Gart.* 22: 57–73.
- MOSS, M.L. 1969. Comparative histology of dermal sclerifications in reptiles. *Acta Anat.* 73: 510–533.
- OTTO, H. 1909. Die Beschuppung de Brevilinguier und Ascalaboten. *Jena. Z. Naturwiss.* 44: 193–252.
- READ, R. 1986. Osteoderms in the Lacertilia: an investigation into the structure and phylogenetic implications of dermal bone found under the skin of lizards. 142 p. MSc thesis, California State University, Fullerton, CA, USA.
- RICHTER, A. 1994. Lacertilien aus der Unteren Kreide von Uña and Galve (Spanien) und Anoual (Marokko). *Berliner geowiss. Abh.* 14: 1–147.
- SCHERZ, M.D., J.D. DAZA, J. KÖHLER, M. VENCES & F. GLAW. 2017. Off the scale: a new species of fish-scale gecko (Squamata: Gekkonidae: *Geckolepis*) with exceptionally large scales. *PeerJ* 5: e2955.
- SCHMIDT, W.J. 1911. Beobachtungen an der Haut von *Geckolepis* und einigen anderen Geckoniden. In A. VOELTZKOW (Ed.), *Reise in Ostafrika in den Jahren 1903–1905 mit Mitteln der Hermann und Elise geb. Hickman Wentzel-Stiftung ausgeführt Wissenschaftliche Ergebniss von Alfred Voeltzkkow*, vol. 4, Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, BW, pp. 331–352.
- SCHMIDT, W.J. 1912. Studien am Integument der Reptilien. I. Die Haut der Geckoniden. *Z. Wiss. Zool.* 51: 139–258.
- SCHUBERT, C. & E. CHRISTOPHERS 1985. “Dermolytische Schreckhäutung”—ein besonderes Autotomieverhalten von *Geckolepis typica* (Reptilia, Gekkonidae). *Zool. Anz.* 214: 129–141.
- SCHUBERT, C., T. STEFFEN & E. CHRISTOPHERS 1990. Weitere Beobachtungen zur “dermolytischen Schreckhäutung” bei *Geckolepis typica* (Reptilia, Gekkonidae). *Zool. Anz.* 224: 175–192.
- SEIDEL, M.R. 1979. The osteoderms of the American alligator and their functional significance. *Herpetologica* 35: 375–380.
- SENSALE, S., W. JONES & R.E. BLANCO 2014. Does osteoderm growth follow energy minimization principles? *J. Morphol.* 275: 923–932.

- STANLEY, E.L., A.M. BAUER, T.J. JACKMAN, W.R. BRANCH & P.L.F.N. MOUTON 2011. Between a rock and a hard polytomy: rapid radiation in the rupicolous girdled lizards (Squamata: Cordylidae). *Mol. Phylogenet. Evol.* 58: 52–70.
- STANLEY, E.L., L.M.P. CERIACO, S. BANDEIRA, H. VALERIO, M.F. BATES & W.R. BRANCH 2016. A review of *Cordylus machadoi* (Squamata: Cordylidae) in southwestern Angola, with the description of a new species from the Pro-Namib desert. *Zootaxa* 4061: 201–226.
- SZCZERBAK, N.N. & M.L. GOLUBEV 1986. The Gekkonid Fauna of the U.S.S.R. and Adjacent Countries [in Russian]. Naukova Dumka Publishing House, Kiev, Ukraine.
- VICKARYOUS, M.K. & B.K. HALL 2008. Development of the dermal skeleton in *Alligator mississippiensis* (Archosauria, Crocodylia) with comments on the homology of osteoderms. *J. Morphol.* 267: 1273–1283.
- VICKARYOUS, M.K. & J.-Y. SIRE 2009. The integumentary skeleton of tetrapods: origin, evolution, and development. *J. Anat.* 214: 441–464.
- VICKARYOUS, M.K., G. MELDRUM & A.P. RUSSELL 2015. Armored geckos: a histological investigation of osteoderm development in *Tarentola* (Phyllodactylidae) and *Gekko* (Gekkonidae) with comments on their regeneration and inferred function. *J. Morphol.* 276: 1345–1357.
- WERNER, F. 1896. Über die Schuppenbekleidung des regenerirten Schwanzes bei Eidechsen. *Sitzber. Akad. Wiss. Wien.* 105: 123–146.
- ZYLBERBERG, L. & J. CASTANET 1985. New data on the structure and growth of the osteoderms in the reptile *Anguis fragilis* L. (Anguidae, Squamata). *J. Morphol.* 186: 327–342.
- ZYLBERBERG, L. & M.H. WAKE 1990. Structure of the scales of *Dermophis* and *Microcaecilia* (Amphibia: Gymnophiona), and a comparison to dermal ossifications of other vertebrates. *J. Morphol.* 206: 25–43.
- ZYLBERBERG, L., J. GERAUDIE, F. MEUNIER & J.-Y. SIRE 1992. Biomineralization in the integumental skeleton of the living lower vertebrates. In B.K. HALL (Ed.), *Bone*, Vol. 4: Bone metabolism and mineralization. CRC Press Boca Raton, FL, pp. 171–224.

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