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A review of the osteoderms of lizards (Reptilia: Squamata)

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ABSTRACT

Osteoderms are mineralised structures consisting mainly of calcium phosphate and collagen. They form directly within the skin, with or without physical contact with the skeleton. Osteoderms, in some form, may be primitive for tetrapods as a whole, and are found in representatives of most major living lineages including turtles, crocodilians, lizards, armadillos, and some frogs, as well as extinct taxa ranging from early tetrapods to dinosaurs. However, their distribution in time and space raises questions about their evolution and homology in individual groups. Among lizards and their relatives, osteoderms may be completely absent; present only on the head or dorsum; or present all over the body in one of several arrangements, including non-overlapping mineralised clusters, a continuous covering of overlapping plates, or as spicular mineralisations that thicken with age. This diversity makes lizards an excellent focal group in which to study osteoderm structure, function, development and evolution. In the past, the focus of researchers was primarily on the histological structure and/or the gross anatomy of individual osteoderms in a limited sample of taxa. Those studies demonstrated that lizard osteoderms are sometimes two-layered structures, with a vitreous, avascular layer just below the epidermis and a deeper internal layer with abundant collagen within the deep dermis. However, there is considerable variation on this model, in terms of the arrangement of collagen fibres, presence of extra tissues, and/or a cancellous bone core bordered by cortices. Moreover, there is a lack of consensus on the contribution, if any, of osteoblasts in osteoderm development, despite research describing patterns of resorption and replacement that would suggest both osteoclast and osteoblast involvement. Key to this is information on development, but our understanding of the genetic and skeletogenic processes involved in osteoderm development and patterning remains minimal. The most common proposition for the presence of osteoderms is that they provide a protective armour. However, the large morphological and distributional diversity in lizard osteoderms raises the possibility that they may have other roles such as biomechanical reinforcement in response to ecological or functional constraints. If lizard osteoderms are primarily for defence, whether against predators or conspecifics, then this 'bony armour' might be predicted to have different structural and/or mechanical properties compared to other hard tissues (generally intended for support and locomotion). The cellular and biomineralisation mechanisms by which osteoderms are formed could also be different from those of other hard tissues, as reflected in their material composition and nanostructure. Material properties, especially the combination of malleability and resistance to impact, are of interest to the biomimetics and bioinspired material communities in the development of protective clothing and body armour. Currently, the literature on osteoderms is patchy and is distributed across a wide range of journals. Herein we present a synthesis of current knowledge on lizard osteoderm evolution and distribution, micro- and macrostructure, development, and function, with a view to stimulating further work.

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Key words: osteoderms, dermal skeleton, lizard, Squamata, development, function, evolution, armour

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I. INTRODUCTION

Vertebrate skin is a large organ that supports and protects the body, and provides the interface between an animal and its environment. The skin consists of two layers – the epidermis (derived from ectoderm) and the underlying dermis (originating from mesoderm and the neural crest), separated by a fibrous basement membrane. In amniotes (reptiles, including birds, and mammals), cells of the epidermis are invested with intermediate filament keratins (formerly α-keratin) across all taxa and additionally corneous beta-protein (CBP, formerly β-keratin) in reptiles and birds (Greenwold *et al.*, 2014; Holthaus *et al.*, 2018). The outermost layer of the epidermis or stratum corneum, consists of anucleated keratinocytes with a cornified lipid envelope in place of the plasma membrane. The underlying dermis is bilaminar, and organised into superficial (stratum superficiale or papillary) and deep (stratum compactum or reticular) layers. The dermis includes various sense organs, nerves and blood vessels, and variable amounts of glandular and fatty tissue. These structures are supported, especially in amniotes, by a meshwork of collagen and elastin fibres forming a loose flexible connective tissue. However, in many vertebrates, plates or nodules of rigid tissue develop within the dermis, composed of varying amounts of organic (e.g. collagen) and inorganic (hydroxyapatite) material.

Among 'fish' (including cyclostomes, actinopterygians, chondrichthyans, and non-tetrapodan sarcopterygians), the components of the dermal skeleton are termed scales and range from thick mineralised plates (e.g. extant sturgeons and gars), through thinner elasmoid scales (e.g. living lungfish), to the thin, weakly mineralised scales of many modern bony (actinopterygian) fish, and the tooth-like placoid scales of sharks and rays (e.g. Sire, Donoghue & Vickaryous, 2009; Witzmann, 2011; Schultze, 2016; Mondejar-Fernandez, 2018). In most fish, the scale is made up of two primary components. The more superficial part is a hard protective hypermineralised layer (cell poor, collagen poor, avascular) of variable thickness and composition (ganoine, hyaloine, enameloid) that forms close to the epidermal–dermal interface (Zylberberg *et al.*, 1992). The formation of this tissue is thought to involve interactions between dermis and epidermis (ectoderm–mesoderm) (e.g. Reif, 1982; Sire *et al.*, 2009), possibly with epidermal cell contributions (but see Mongera & Nüsslein-Volhard, 2013). Underlying the hypermineralised layer are deeper layers of less dense, collagen-rich, vascularised tissue. Depending on the thickness and arrangement of these two tissue layers, fish scales may be termed elasmoid (most living fish), ganoid (living birchirs and gars), cosmoid (extinct lungfish and their relatives), or placoid (sharks, rays and related groups).

Scales were retained in stem- and early tetrapods (e.g. *Tiktaalik*, *Acanthostega*), particularly on the ventral surface of the body (gastral scales) but often also dorsally (Witzmann, 2009, 2011). Whether these integumentary structures are termed scales or osteoderms (ODs) in tetrapods, and the nature of the distinction between the two, is something of a moot point (Castanet *et al.*, 2003; Vickaryous & Sire, 2009), but there is a general agreement that, in tetrapods, integumentary structures generally lack the hypermineralised layer found in most fish. Nonetheless, the tendency to form mineralisations within the skin is

evidently an ancient trait, although it is variably expressed in terrestrial vertebrates.

In crown-group tetrapods, ODs vary in size, shape, and distribution, often within a single individual. They make up a significant yet somewhat understudied area of the evolutionary history of the tetrapod skeleton, and generally provide the only evidence of the skin structure in fossil taxa. ODs have been lost and regained in different tetrapod lineages through geological time (Hill, 2005). They were retained in many extinct groups of amphibians [lepospondyls, non-lissamphibian temnospondyls (e.g. Witzmann & Soler-Gijón, 2010; Witzmann, 2011; Buchwitz *et al.*, 2012)] and although they have been lost in most thin-skinned living amphibians, they are expressed in some frogs (Ruibal & Shoemaker, 1984). Mineralisations are also found in the skin of some caecilians (Wake, 1975; Zylberberg, Castanet & de Ricqlès, 1980; Zylberberg & Wake, 1990), although it remains unclear if these elements are homologous with ODs (Vickaryous & Sire, 2009).

ODs are more common in amniotes (Hill, 2005; Vickaryous & Sire, 2009) and stem-amniotes (e.g. Chroniosuchidae; Buchwitz *et al.*, 2012). They have been recorded in representative species of many reptilian lineages including parareptiles [e.g. parieasaurs, procolophonids (Cisneros, 2008; Scheyer & Sander, 2009)], turtles (e.g. Barrett *et al.*, 2002; Clarac *et al.*, 2020), crocodylians (e.g. Seidel, 1979; Frey, 1988; Vickaryous & Hall, 2008; Hill, 2010; Dubansky & Dubansky, 2018), non-avian dinosaurs (e.g. de Buffrénil, Farlow & de Ricqlès, 1986; Dodson *et al.*, 1998; de Ricqlès *et al.*, 2001; Scheyer & Sander, 2004; Main *et al.*, 2005; D'Emic, Wilson & Chatterjee, 2009; Rogers *et al.*, 2011; Burns & Currie, 2014; Brown, 2017; Vidal *et al.*, 2017), other archosaurs (e.g. Cerda & Desojo, 2010; Cerda *et al.*, 2013, 2015; Scheyer, Desojo & Cerda, 2014; Cerda, Desojo & Scheyer, 2018), the sauropterygian placodonts (e.g. Scheyer, 2007), and lepidosaurs (discussed in Section II.1). They are also recorded in some mammals [e.g. armadillos, glyptodonts, mylodontid sloths (Hill, 2006; Vickaryous & Hall, 2006; McDonald, 2018)] and in early non-mammalian synapsids [e.g. *Elliotsmithia longiceps* (Reisz, Dilkes & Berman, 1998); see also Botha-Brink & Modesto, 2007].

Squamates (lizards, including amphisbaenians, and snakes) are a large and successful reptilian group with more than 10,000 species and a near-global distribution. They show a diversity of body size and morphology, occupy multiple ecological niches, and have a long evolutionary history (over 250 million years). ODs have been lost in snakes and amphisbaenians, but are present in many clades of lizards including Scincidae, Cordylidae, Gerrhosauridae, Anguidae, Lacertidae, Helodermatidae, and Varanidae (Fig. 1). By far the greatest diversity of tetrapod ODs, in terms of shape, distribution, and expression, is found in lizards (Vickaryous & Sire, 2009), making them an ideal group in which to study OD evolution, development, and function. Our aim in this review is to collate current knowledge of squamate ODs, as a foundation and stimulus for further work.

II. EVOLUTIONARY HISTORY AND DISTRIBUTION IN SQUAMATES

(1) Evolutionary history

The reptilian group Lepidosauria comprises Rhynchocephalia and Squamata, sister clades that separated from one another at least 230 million years ago (e.g. Jones *et al.*, 2013). Lepidosauromorpha (Lepidosauria and its stem taxa) is the sister group of Archelosauria, encompassing turtles and archosaurs (Crawford *et al.*, 2015) within neodiapsid reptiles. Today, Rhynchocephalia is represented by a single species, *Sphenodon punctatus*, the Tuatara of New Zealand, whereas Squamata consists of more than 10,000 species of lizards, snakes, and amphisbaenians grouped, on molecular data (e.g. Pyron, Burbrink & Wiens, 2013; Zheng & Wiens, 2016; Burbrink *et al.*, 2020; but *contra* Losos, Hillis & Greene, 2012), into Gekkota, Dibamidae, Scincoidea (Scincidae, Cordyliformes, Xantusiidae), Lacertoidea (Teiioidea, Lacertidae, Amphisbaenia), and Toxicofera (Iguania, Anguimorpha, Serpentes) (Fig. 1). There remains uncertainty as to whether Gekkota, Dibamidae, or both, represent the first major branches from the squamate crown (e.g. Pyron *et al.*, 2013; Burbrink *et al.*, 2020).

The early fossil record of rhynchocephalians is relatively good (Jones *et al.*, 2013), but ODs have only been recorded once, in the Early Cretaceous (~120 million years ago) species *Pamizinsaurus tlayuaensis* from the Tlayúa Formation in Puebla, Mexico (Reynoso, 1997). The generic name *Pamizinsaurus* stems from a Nahuatl word pamizintl, meaning corn, which refers to the bead-like ODs covering the body and giving the appearance of a corn-cob (Reynoso, 1997). However, no other rhynchocephalian has been found with any trace of ODs, despite several complete skeletons. Moreover, ODs have not been recorded in any of the species currently placed on the lepidosaurian stem, although this may be an artefact of a poor fossil record and incomplete specimens. Given the widespread occurrence of ODs in Archelosauria, it seems likely that OD development was suppressed in stem-lepidosaurs, with re-expression occurring rarely in rhynchocephalians and more widely in squamates.

Although molecular divergence estimates (e.g. Jones *et al.*, 2013) place the origin of squamates into the early-mid Triassic (supported by records of middle Triassic rhynchocephalians), there are no unequivocal records of squamates until the Middle Jurassic (UK, Russia, China, Central Asia). Most of these early lizard specimens are represented by isolated elements, making it difficult to be certain whether ODs were present. However, *Changetisaurus estesi* (Middle Jurassic, Kyrgyzstan; Fedorov & Nessov, 1992), reportedly has a cover of rectangular ODs, as does an as-yet unnamed lizard specimen from the Middle Jurassic of China (Conrad *et al.*, 2013). The phylogenetic position of neither lizard is certain, but they may be related to Paramacellodidae, a fossil group better known from Jurassic and Early Cretaceous deposits across northern continents (North America, Europe, Asia; Evans & Chure, 1998). Paramacellodids are typically

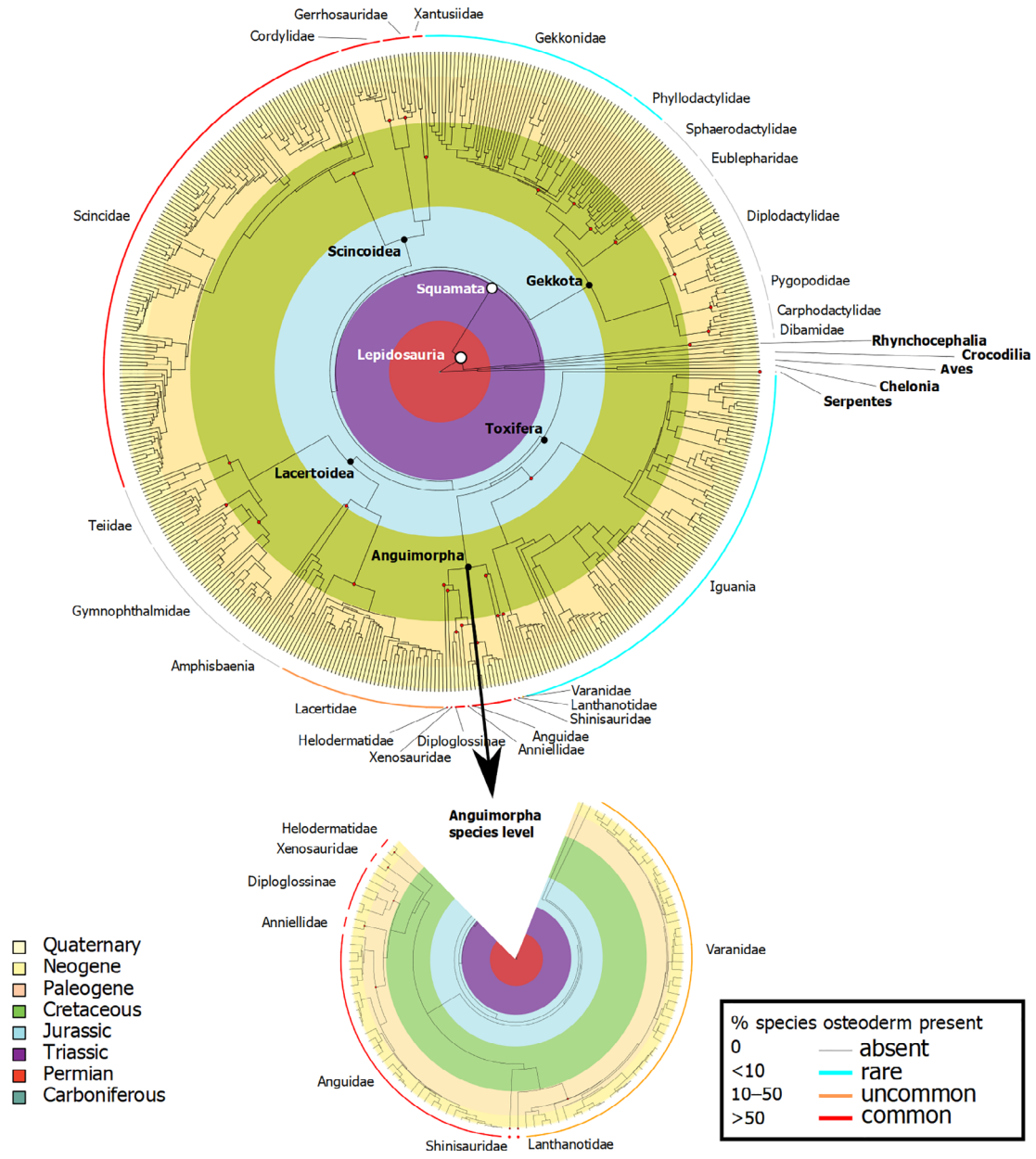

Fig. 1. A time-calibrated phylogeny, modified from Zheng & Wiens (2016) showing osteoderm (OD) abundance across extant lizard genera as taken from the literature, plotted over geological era, with outgroups. An expanded species-level phylogeny is shown for Anguimorpha. Abundance is estimated as the proportion (% of species) within a clade that develop ODs: common, >50%; uncommon, 10–50%; rare, <10%. Prepared in R using packages phytools (Revell, 2012), Geiger (Pennell *et al.*, 2014), ape (Paradis & Schliep, 2019), and plotrix (Lemon, 2013).

placed on the stem of Scincoidea, and like many living scincoids they bore a complete covering of imbricating rectangular ODs [e.g. *Sharovisaurus karatauensis*, Upper Jurassic, Kazakhstan (Hecht & Hecht, 1984; see also Richter, 1994)]. *Hongshanxi xiei* (Mid-Upper Jurassic, China; Dong *et al.*, 2019) also has ODs, but they are restricted to the temporal region of the skull and vary in their size and shape [as also seen in some (unrelated) modern lacertids]. ODs have been reported in several other Cretaceous lizards including the Early Cretaceous *Scandensia ciervensis* [Spain (Bolet & Evans, 2011), cycloid ODs], and *Yabeinosaurus robustus* [China (Dong, Wang & Evans, 2017), small, scattered ODs], and several Late Cretaceous taxa including: the scincoid *Parmeosaurus scutatus* [Late Cretaceous, China (Dong *et al.*, 2018), complete cover of imbricate rectangular ODs single dorsally, and binary (= two ODs joined into a

compound structure) ventrally], the cordyliform *Konkasaurus mahalana* [Madagascar (Krause, Evans & Gao, 2003), rectangular ODs]; and several monstersaurs [*Gobiderma pulchrum*, Mongolia (Borsuk-Białynicka, 1984; Conrad *et al.*, 2011); *Chianghsia nankangensis*, China (Mo, Xu & Evans, 2012)]. Post Cretaceous–Paleogene (K–P) boundary, there are numerous records of Paleogene and Neogene squamate taxa with ODs, notably among Anguimorpha [e.g. glyptosaurines (de Buffrénil, Sire & Rage, 2010; de Buffrénil *et al.*, 2011); anguids and anniellids (Estes, 1983); helodermatids (Mead *et al.*, 2012); 'necrosaurs' (Estes, 1983; Smith & Habersetzer, 2021)] and Scincoidea (e.g. Gerrhosauridae; Estes, 1983).

(2) Distribution of osteoderms in living lizard taxa

Amongst extant lizard taxa, ODs have been reported for many taxa (up to 25% of species; see Table 1), although their presence is not necessarily universal within even a single genus (e.g. *Varanus*; Erickson *et al.*, 2003). ODs are common among scincids (Camp, 1923; Camaiti *et al.*, 2019), gerrhosaurids (Camp, 1923; Nance, 2007), cordylids (Broeckhoven *et al.*, 2015; Stanley, 2016; Broeckhoven, du Plessis & Hui, 2017b; Broeckhoven, De Kock & Le Fras Nortier Mouton, 2017*a*; Broeckhoven *et al.*, 2018*a*), xenosaurids (Gao & Norell, 1998; Bhullar, 2011), helodermatids (Moss, 1969; Maisano *et al.*, 2019; Kirby *et al.*, 2020; Iacoviello *et al.*, 2020), anguids (Hoffstetter, 1962; Strahm & Schwartz, 1977; Zylberberg & Castanet, 1985; Levrat-Calviac *et al.*, 1986; Bochaton *et al.*, 2015), anniellids (Bhullar & Bell, 2008), shinisaurids (Bever *et al.*, 2005; Conrad *et al.*, 2014), and lanthanotids (McDowell & Bogert, 1954; Maisano *et al.*, 2002, 2019). ODs are also found in some (but not all) species of varanids (Erickson *et al.*, 2003; Maisano *et al.*, 2019; Kirby *et al.*, 2020) and lacertids (Estes *et al.*, 1988; Borsuk-Białynicka *et al.*, 1999; Constantini & Dell'Omo, 2010). ODs are virtually absent from iguanians with two published exceptions, a species of leaf chameleon (*Brookesia perarmata*) and some individual specimens of the marine iguana (*Amblyrhynchus cristatus*) (de Queiroz, 1987; Schucht *et al.*, 2020). ODs are rare in gekkotans, but have been reported from a small number of species across two different clades: Gekkonidae and Phyllodactylidae (Schmidt, 1912*a*; Levrat-Calviac, 1986; Levrat-Calviac & Zylberberg, 1986; Vickaryous *et al.*, 2015; Paluh *et al.*, 2017; Scherz *et al.*, 2017; Laver *et al.*, 2020). It is worth noting that small, superficially OD-like elements have been described for two genera of sphaerodactylid geckos (*Aristelliger* and *Teratoscincus*) (Bauer & Russell, 1989; Griffing *et al.*, 2018). These irregularly shaped elements, known as parafrontal bones, form within a layer of connective tissue above the orbit but deep to the dermis. Hence, they are considered to be separate ossifications (Bauer & Russell, 1989; Griffing *et al.*, 2018). ODs are absent from snakes and the specialised burrowing groups Amphisbaenia and Dibamidae.

III. OSTEODERM MACRO- AND MICROSTRUCTURE

(1) Macrostructure

Until recently, most reports of lizard OD morphology (i.e. macrostructure) were derived from the study of dried skeletal elements or diaphonised skin stained with Alizarin red (e.g. Strahm & Schwartz, 1977). However, since the early 2000s computed tomography (CT) scanning has become the leading tool for the study of the size, shape, and *in situ* distribution of ODs. CT scanning is non-invasive, able to generate high-resolution two-dimensional and three-dimensional data rapidly, and can be used to map the distribution of ODs across body regions or the entire lizard (e.g. Maisano *et al.*, 2002; Bever *et al.*, 2005; Paluh *et al.*, 2017; Maisano *et al.*, 2019; Laver *et al.*, 2020; Iacoviello *et al.*, 2020), as reviewed in Broeckhoven & du Plessis (2018). Further, there are several open-source repositories of CT data archiving OD-bearing lizards, including Digimorph (digimorph.org) and Morpho Source (morphosource.org). The potential for integrating the spatial morphological information with that provided by classical histology and functional modelling is currently being explored in several groups (Iacoviello *et al.*, 2020)

Lizard ODs vary in size, shape, and body-wide distribution (Fig. 2). For example, whereas ODs are typically confined to the head of some lacertids (Fig. 2F), their distribution is more pervasive in many scincids, anguids, and cordyliforms (Fig. 2A–C). In these groups, ODs may form a comprehensive body-wide covering of imbricating or interlocking rectangular or cycloid plates, or may be confined to specific regions due to differing selective pressures (Camp, 1923; Richter, 1994; Stanley, 2013, 2016; Broeckhoven *et al.*, 2015, 2017*a*, 2017*b*; Broeckhoven *et al.*, 2018*a*) (Figs 2 and 3). In some species, individual ODs may fuse together, creating compound mosaics (Fig. 3C), tessellations (Fig. 2E) or mats of bone (e.g. skeletally mature gekkotans and *Varanus komodoensis*; Paluh *et al.*, 2017; Maisano *et al.*, 2019), or even fuse with the underlying cranial bones [-e.g. cordylids, gerrhosaurids, xenosaurids, lacertids, some scincids, and helodermatids (Bhullar, 2011; Dubke, Hipsley & Müller, 2018; Maisano *et al.*, 2019)]. Variation also occurs across ontogenetic series, as outlined in Section IV.

As a class of skeletal element, ODs are highly polymorphic, even within the same species or individual (Erickson *et al.*, 2003; Vickaryous *et al.*, 2015; Maisano *et al.*, 2019). For example, in *V. komodoensis* there are four distinct OD morphotypes across the head alone: rosette, platy, dendritic, and vermiform (Maisano *et al.*, 2019). Similarly, across the body of *Cordylus namakuiyus*, ODs vary in overall shape (rectangular to circular), and in the presence and sharpness of their keel (Stanley, 2016) (Fig. 2A). Other OD morphologies include simple granular bones (e.g. postcranial ODs in *Tarentola* spp.; Vickaryous *et al.*, 2015; Fig. 4), keeled plates (e.g. fossil varanoid 'necrosaurs'; Estes, 1983), spherical or globose studs [e.g. *Heloderma* (Mead *et al.*, 2012; Iacoviello

Table 1. Osteoderms reported in the literature for extant lizards

Taxon		Number of extant species[a]	Taxonomic distribution of osteoderms within the clade[b]	Key references
Dibamidae		25	Absent	
Gekkota	Eublepharidae	40	Absent	Levrat-Calviac & Zylberberg (1986); Levrat-Calviac, Castanet & Zylberberg (1986); Vickaryous, Meldrum & Russell (2015); Paluh, Griffing & Bauer (2017); Scherz *et al.* (2017); Laver *et al.* (2020).
	Gekkonidae	1356	Rare (3 spp.; *Gekko gecko*, *G. reevesii*, *Geckolepis maculata*)	
	Carphodactylidae	32	Absent	
	Diplodactylidae	155	Absent	
	Phyllodactylidae	151	Rare (at least 6 spp. of *Tarentola*)	
	Sphaerodactylidae	228	Absent	
	Pygopodidae	46	Absent	
Scincoidea	Scincidae	1709	Common	Camp (1923); Oliver (1951); Paluh & Bauer (2017); Camaiti *et al.* (2019)
	Gerrhosauridae	37	Common	Camp (1923); Nance (2007)
	Cordylidae	70	Common	Broeckhoven, Diedericks & Le Fras Nortier Mouton (2015); Broeckhoven *et al.* (2018*a*)); Stanley (2016)
	Xantusiidae	35	Common	Strahm & Schwartz (1977)
Lacertoidea	Lacertidae	350	Uncommon	Estes, De Queiroz & Gauthier (1988); Arnold (1989); Arnold, Arribas & Carranza (2007); Barahona & Barbadillo (1998); Borsuk-Białynicka, Lubka & Böhme (1999); Constantini & Dell'Omo (2010)
	Amphisbaenia	201	Absent	
	Teiidae	170	Absent	
	Alopoglossidae	28	Absent	
	Gymnophthalmidae	267	Absent	
Toxifera	Iguania	1968	Rare (reported for only 2 spp.; *Brookesia perarmata* and *Amblyrhynchus cristatus*)	de Queiroz (1987); Schucht *et al.* (2020)
	Helodermatidae	5	Common	Moss (1969); Maisano *et al.* (2019); Kirby *et al.* (2020); Iacoviello *et al.* (2020)
	Xenosauridae	12	Common	Hoffstetter (1962); Strahm & Schwartz (1977);
	Diploglossidae	51	Common	Zylberberg & Castanet (1985); Good & Schwenk (1985); Bochaton *et al.* (2015)
	Anniellidae	6	Common	Bhullar & Bell (2008)
	Anguidae	85	Common	Gao & Norell (1998);
	Shinisauridae	1	Common	Bhullar (2011)
	Lanthanotidae	1	Common	Bever, Bell & Maisano (2005);
	Varanidae	83	Uncommon to rare	Conrad, Head & Carrano (2014) McDowell & Bogert (1954); Maisano *et al.* (2002, 2019) Erickson *et al.* (2003); Maisano *et al.* (2019); Kirby *et al.* (2020)
	Serpentes	3789	Absent	

[a]Species numbers from Uetz, Freed & Hošek (2020).
[b]Based on the literature, we estimated the proportion (% of species) within a clade that develop osteoderms: common, >50%; uncommon, 10–50%; rare, <10% (Fig. 1).

et al., 2020; Kirby *et al.*, 2020); Figs 3A and 4), interlocking tesserae [cranial ODs in *Gekko gecko*, Fig. 2E (Vickaryous *et al.*, 2015; Laver *et al.*, 2020)], cycloid [*Geckolepis* (Schmidt, 1912*a*; Paluh *et al.*, 2017)] or palmate shapes (*Anniella* spp.; Bhullar & Bell, 2008), and compound elements consisting of multiple plates joined together [e.g. scincids (Otto, 1909; Camp, 1923; Estes *et al.*, 1988); Fig. 3C]. The terminology of individual OD element morphology has also been variable across individual publications and may benefit from a systematic approach.

While ODs are firmly anchored within the dermis (discussed in Section IV.2), in at least two species of gecko, they can also be shed. *Geckolepis* is an arboreal genus of fish-scaled gecko capable of regional integumentary loss (Paluh *et al.*, 2017; Scherz *et al.*, 2017). Regional integumentary loss is a dramatic antipredation mechanism where the skin can be

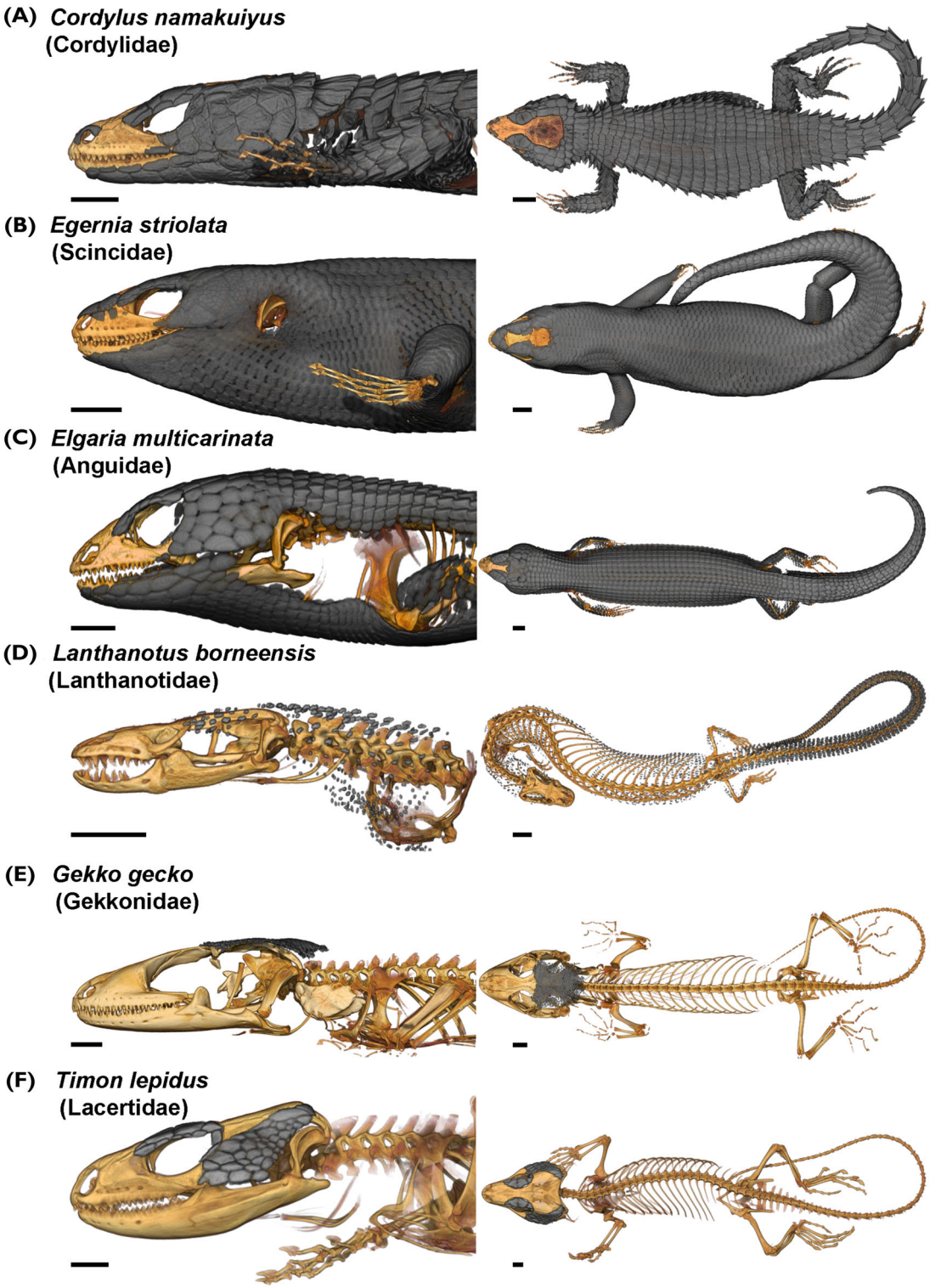

Fig. 2. Osteoderm shape and location patterns in six lizard species from different families. Computed tomography (CT) reconstructions of the bones (orange) and osteoderms (grey) in (A) *Cordylus namakuiyus* (Cordylidae), (B) *Egernia striolata* (Scincidae), (C) *Elgaria multicarinata* (Anguidae), (D) *Lanthanotus borneensis* (Lanthanotidae), (E) *Gekko gecko* (Gekkonidae), and (F) *Timon lepidus* (Lacertidae). Left lateral view of the cranium and the most rostral part of the body (left) and dorsal view of the whole body (right). Note that the specimen of *T. lepidus* presented here had no post-cranial osteoderms; osteoderm covering of the body is susceptible to ontogenetic changes in every species. Osteoderms covering of the frontal and parietal bones were only represented in grey when they were distinct (not fused) from the bone in the X-ray pictures to avoid overinterpretation of the data. CT-scan data were downloaded from MorphoSource. Scale bars: 5 mm.

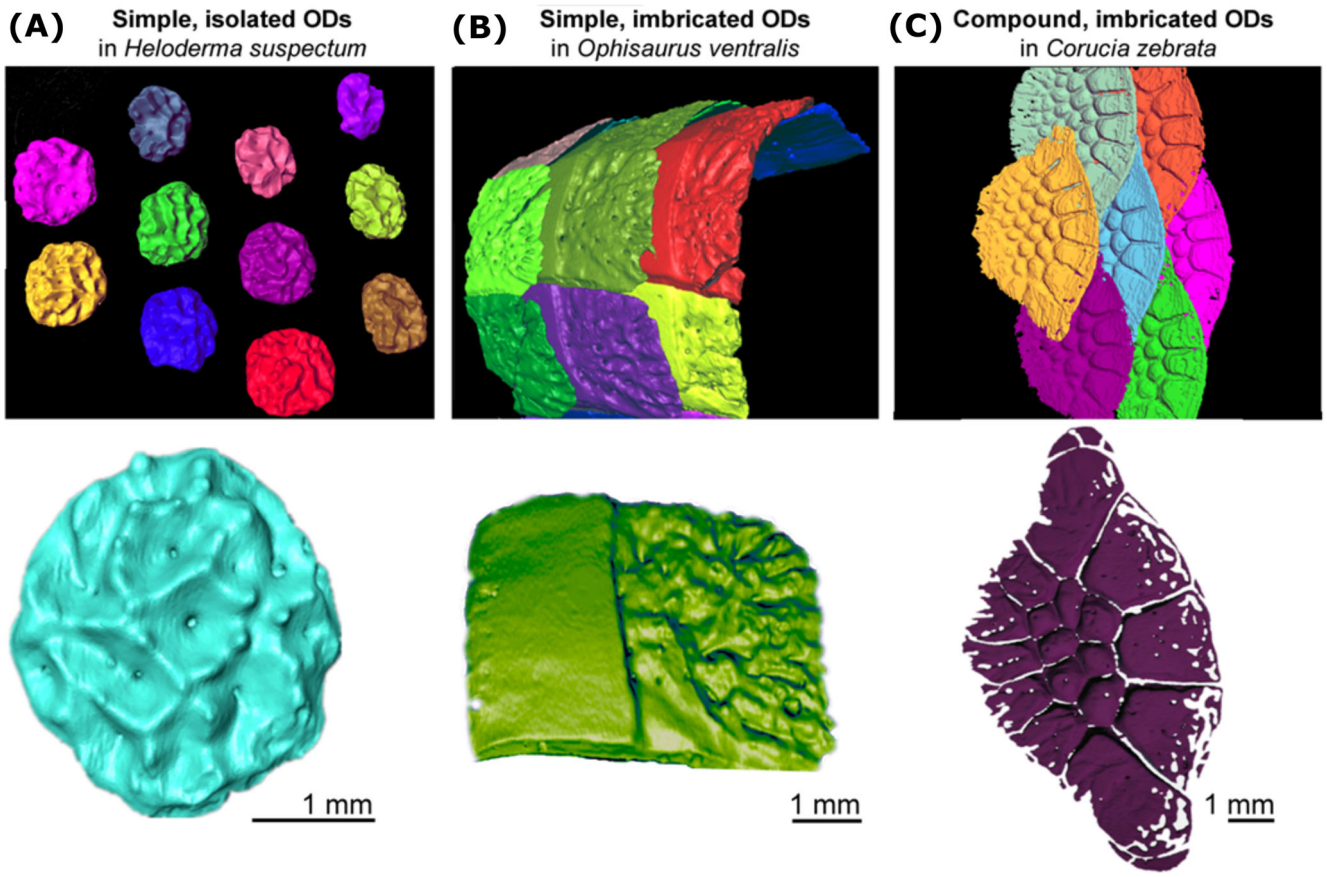

Fig. 3. Shapes and distribution pattern of some dorsal skin osteoderms (ODs) in three species of lizards. Dorsal views of the distribution of neighbouring osteoderms (top) and the morphology of isolated osteoderms (bottom) in (A) *Heloderma suspectum* (Helodermatidae), (B) *Ophisaurus ventralis* (Anguidae), and (C) *Corucia zebrata* (Scincidae).

avulsed to escape predation (Bauer, Russell & Shadwick, 1989, 1992; Paluh *et al.*, 2017). Similar to tail autotomy, regional integumentary loss is associated with pre-existing planes of weakness that partially divide the dermis (Bauer *et al.*, 1989, 1992). When the gecko is grasped, it can slough a portion of its epidermis and superficial dermis, along with any associated ODs.

(2) Microstructure

At the level of histology, ODs are typically heterogeneous in their composition, including bone, mineralised and unmineralised collagen fibre bundles, blood vessels, nerves, and yellow marrow (Fig. 4) (Moss, 1969; Strahm & Schwartz, 1977; Zylberberg & Castanet, 1985; Vickaryous & Sire, 2009; de Buffrénil *et al.*, 2010; Bochaton *et al.*, 2015; Broeckhoven *et al.*, 2017*b*; Iacoviello *et al.*, 2020; Kirby *et al.*, 2020). Moreover, the bone tissue and its fibrillary matrix often varies, even within a single OD. This diversity includes both cancellous and compact bone, spatially organised into woven-fibred, parallel-fibred and lamellar matrices (Moss, 1969; Scheyer, 2007; de Buffrénil *et al.*, 2010; Vickaryous & Sire, 2009). The cortical borders of ODs may also become enriched with Sharpey's fibres, giving rise to Sharpey-fibred bone, an ossified matrix heavily invested with extrinsic collagenous fibres (Moss, 1969; Strahm & Schwartz, 1977; de Buffrénil *et al.*, 2011; Vickaryous *et al.*, 2015; Kirby *et al.*, 2020).

Until recently, details of lizard OD bone histology were known for only three species, the anguimorphs *Heloderma suspectum* and *Anguis fragilis*, and the gekkotan *Tarentola mauritanica* (Schmidt, 1912*a*, 1912*b*, 1914*a*; Moss, 1969; Zylberberg & Castanet, 1985; Levrat-Calviac *et al.*, 1986; Levrat-Calviac & Zylberberg, 1986). However, renewed interest in OD microstructure over the last decade is expanding this taxonomic list to include a much broader representation of lizards, including several other species of gekkotans, various scincids and cordylids, a varanid, and even a chamaeleonid (Vickaryous *et al.*, 2015; Broeckhoven *et al.*, 2017*b*; Paluh *et al.*, 2017; Canei & Nonclercq, 2020; Iacoviello *et al.*, 2020; Kirby *et al.*, 2020; Schucht *et al.*, 2020). As a result, a better understanding of how OD histology varies across taxa is beginning to emerge. For example, in the anguid *A. fragilis*, ODs are composed of a superficial layer of woven-fibred bone and a deeper layer or plate of lamellar bone (Zylberberg & Castanet, 1985). By contrast, the bony contribution of

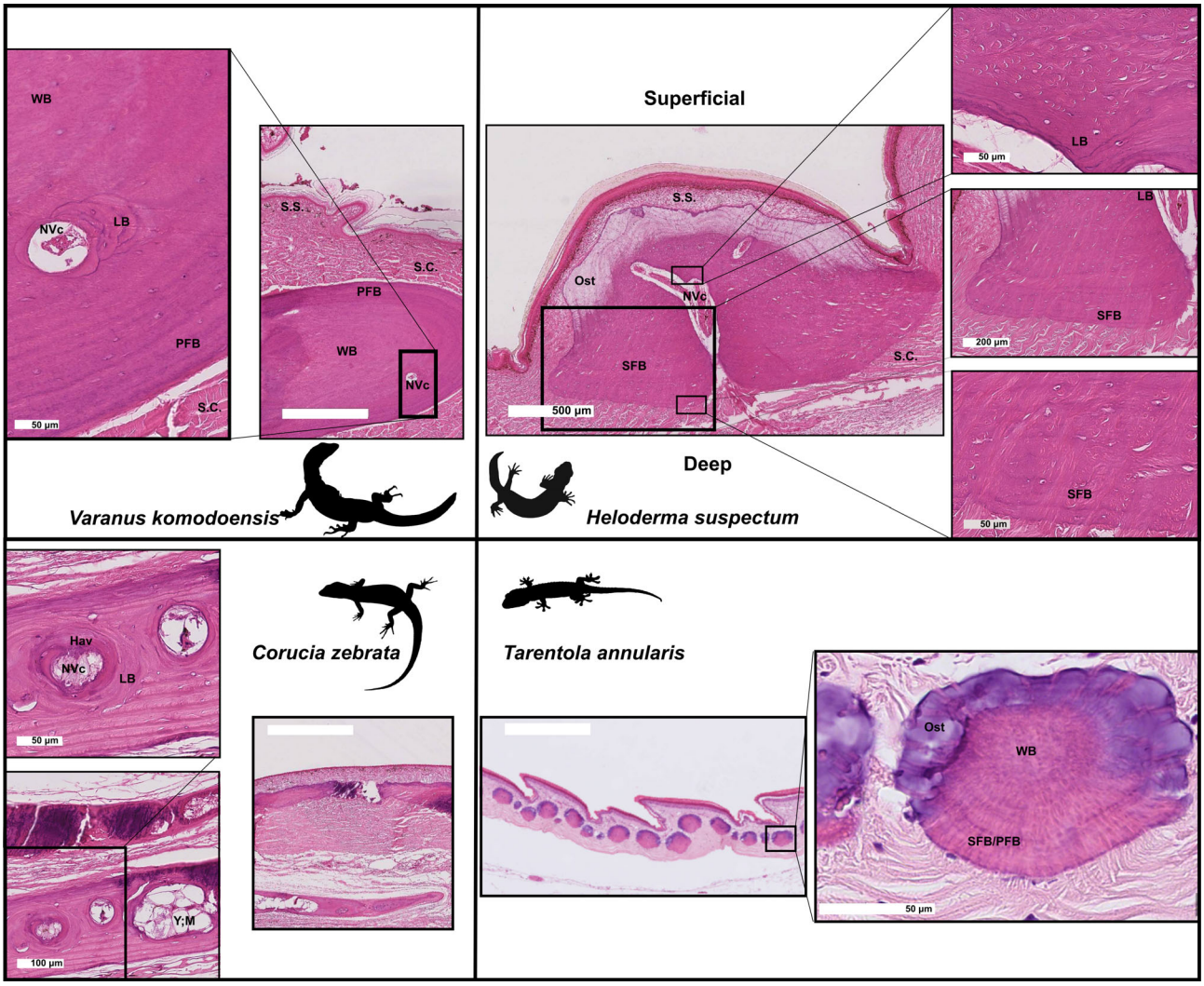

Fig. 4. Histological overview of osteoderms from *Varanus komodoensis*, *Heloderma suspectum*, *Tarentola annularis*, and *Corucia zebrata*, demonstrating diversity of osteoderm size, tissue characteristics and bone fibre patterning. All images stained with haematoxylin and eosin. Hav, Haversian structure; LB, lamellar bone; NVc, neurovascular canal; Ost, osteodermine; PFB, parallel-fibred bone; S.C., stratum compactum; SFB, Sharpey-fibre bone; S.S., stratum superficiale; WB, woven bone; Y; M, yellow marrow. Scale bars: main images all 200 µm; higher magnifications as indicated. *Varanus komodoensis* and *Heloderma suspectum* from the same specimens as Kirby *et al.* (2020).

Heloderma spp. ODs is primarily Sharpey-fibred bone, with lamellar bone only deposited around neurovascular bundles, thus forming secondary osteons (Haversian systems) (Moss, 1969; Iacoviello *et al.*, 2020; Kirby *et al.*, 2020). In the cordylids *Smaug giganteus* and *Ouroborus cataphractus*, each OD consists of an outer cortex of parallel-fibred bone, with a deeper layer of woven-fibred bone and a cancellous core lined with lamellar bone (Broeckhoven *et al.*, 2017*b*). A similar arrangement, with a parallel-fibred bone cortex and a cancellous core lined with lamellar bone was recently described for the chameleon *Brookesia perarmata* (Schucht *et al.*, 2020). The histology of regenerated ODs typically resembles that of the original (e.g. in the geckos *T. annularis* and *T. mauritanica*; Vickaryous *et al.*, 2015). However, in some diploglossine anguids regenerated ODs develop a tissue (Sharpey-fibre bone) not present in the prototypic form (Bochaton *et al.*, 2015).

The large investment of bone in lizard ODs has raised the possibility of using these elements for skeletochronological studies. Although ODs sampled from across the body may hold some utility in this regard (at least in anguids), regenerated ODs are entirely unreliable indices of age (Bochaton *et al.*, 2015; see also Guarino, Mezzasalma & Odierna, 2016). Among crocodylians, for which the use of ODs in skeletochronology has been more intensively studied, the emerging consensus is that the age estimates from the elements should be viewed with caution (Klein, Scheyer & Tütken, 2009). Although cyclical growth marks may be

present, age estimation is complicated by remodelling (e.g. by reproductive-aged females or pathological calcium deficiencies) and/or close spacing of annual bone deposits (Tucker, 1997; Klein *et al.*, 2009).

Among some species, the superficial surface (closest to the epidermis) of the OD is covered by an enigmatic capping tissue (Moss, 1969; de Buffrénil *et al.*, 2011; Vickaryous *et al.*, 2015; Iacoviello *et al.*, 2020; Kirby *et al.*, 2020). This tissue, termed osteodermine (de Buffrénil *et al.*, 2011), is a dense, avascular, cell-poor, hypermineralised enamel-like layer that lacks intrinsic collagen (de Buffrénil *et al.*, 2010, 2011; Vickaryous *et al.*, 2015). To date, osteodermine has only been reported for a few distantly related squamate species, including the anguimorphan *Heloderma suspectum*, the geckos *T. annularis* and *T. mauritanica*, and at least one unnamed fossil glyptosaurine anguid (Moss, 1969; de Buffrénil *et al.*, 2011; Vickaryous *et al.*, 2015; Kirby *et al.*, 2020). A comparable capping tissue has also been reported for the scincids *Scincus* and *Eumeces schneideri* (Canei & Nonclercq, 2020). Available evidence reveals that even among closely related taxa, the expression of osteodermine is irregular. For example, although osteodermine is present in two species of *Tarentola* geckos (*T. annularis* and *T. mauritanica*), it is absent from four others (*T. americana*, *T. crombiei*, *T. chazaliae*, and *T. neglecta*; Levrat-Calviac, 1986; Vickaryous *et al.*, 2015). At the level of histology osteodermine is characterised by a series of concentrically organised periodic growth lines. Unlike most of the osteodermine matrix, these growth lines stain with various connective tissue dyes (Vickaryous *et al.*, 2015). Based on its structural similarity to other hypermineralised tissues (including enamel, ganoine, and hyaloine), osteodermine is predicted to share a comparable mode of development (de Buffrénil *et al.*, 2011). Of these, osteodermine appears to resemble hyaloine most closely, in that both tissues develop at a short distance from the epidermis (Sire, 1993; Sire *et al.*, 2009). Accordingly, osteodermine deposition may involve a dynamic or inductive interaction between the dermis and epidermis (Levrat-Calviac & Zylberberg, 1986; de Buffrénil *et al.*, 2011; Vickaryous *et al.*, 2015; Kirby *et al.*, 2020). Keratin, independent from that of the superficial keratinous scute, has also been recorded in the basal part of the OD in *Heloderma* (Iacoviello *et al.*, 2020).

In addition to routine serial histology, a number of other microscopic and analytical strategies have been employed to study OD structure and composition. These include transmission electron microscopy, scanning electron microscopy, and microradiography (Zylberberg & Castanet, 1985; Levrat-Calviac, 1986; Levrat-Calviac & Zylberberg, 1986), as well as multi-rotation polarised light microscopy (Kirby *et al.*, 2020), atomic force microscopy and finite element analyses (Iacoviello *et al.*, 2020). To date these methods have only been used to investigate a handful of species (*Anguis fragilis*, *Tarentola mauritanica*, and *Heloderma suspectum*). A more comprehensive survey of OD microstructure across a more diverse sample of lizards is needed to provide a broader picture of OD microscopic diversity, and to provide a firmer basis for an understanding of form–function relationship.

IV. DEVELOPMENT

(1) General observations

As for all vertebrates, the epidermis of lizard skin is dominated by keratinocytes, while the underlying dermis is a fibrous mesh of connective tissues invested with blood vessels, and nerves. ODs develop within the dermis, either within the more loosely organised superficial dermis (stratum superficiale) or adjacent to the boundary between the superficial and deep dermis (stratum compactum) (Vickaryous & Sire, 2009; Vickaryous *et al.*, 2015). While the epidermis does not appear to contribute directly to the ossified portion of the OD, it may participate in the formation of the superficial capping tissues (see Section IV.2).

Although their formation is relatively delayed compared to the rest of the skeleton, ODs have been documented among comparatively small, skeletally immature lizards (Schmidt, 1912*a*, 1912*b*, 1914*a*; Vickaryous *et al.*, 2015; Stanley, 2016; Laver *et al.*, 2020). Early OD development takes place asynchronously across the body, and appears to be associated with maturation of the epidermis and dermis (Vickaryous & Sire, 2009). Interestingly, the pattern in which ODs first appear across the body varies among taxa. For example, while OD-bearing geckos and the anguimorph *Heloderma* first develop ODs across the head and cervical regions (Moss, 1969; Vickaryous *et al.*, 2015; Laver *et al.*, 2020), in cordylids they first appear across the tail and along the caudal margins of the head (Stanley, 2016).

(2) Osteoderm development in lizards

OD development is best understood from the study of *Heloderma* (Schmidt, 1912*b*; Moss, 1969; see also Kirby *et al.*, 2020), *Anguis* (Schmidt, 1914*a*) and the gekkotans *Tarentola* and *Gekko* (Schmidt, 1912*a*; Vickaryous *et al.*, 2015; see also Laver *et al.*, 2020). At the level of histology, ODs begin within the dermis as a concentration of dense irregular connective tissue. While cells are present both within and adjacent to these connective tissue primordia, they do not form any obvious aggregations. Further, there is no sign of a placode or any direct involvement of the epidermis. Initially, OD primordia are weakly defined and difficult to distinguish from the fibrous collagen of the surrounding dermis. Primarily, they appear to be variably shaped concentrations of dermis with various associated mineralised collagen fibres (e.g. Schmidt, 1914*a*, 1912*a*, 1912*b*; Vickaryous *et al.*, 2015). As they grow in size, ODs begin to ossify. Although this early mode of ossification is often characterised as direct osseous metaplasia, that is the direct transformation of the pre-existing soft tissue (here the dermis) into bone (*sensu* Haines & Mohuiddin, 1968; Beresford, 1981), detailed investigations of this initial stage of deposition are lacking. Alternatively, lizard ODs may employ a form of intramembranous

ossification as was recently reported for the crocodylian *Alligator mississippiensis* (Dubansky & Dubansky, 2018). Regardless, ODs in lizards develop without a cartilaginous precursor and routinely incorporate large collagen fibres from the surrounding dermis into the bony matrix. These perforating, or Sharpey's, fibres then anchor each OD within the dermis, and even with other adjacent ODs (Moss, 1969; Strahm & Schwartz, 1977; de Buffrénil *et al.*, 2011; Vickaryous *et al.*, 2015).

As growth continues, ODs become increasingly well-defined within the dermis and the matrix becomes dominated by bone of various collagenous organisations. Large extrinsic bundles of unmineralised collagen may also be present passing through the matrix. At this stage, OD development does involve intramembranous ossification, characterised by an enveloping seam of osteoid and osteoblasts. Although the origin of these osteoblasts remains unclear, they are hypothesised to originate from the neural crest (Smith & Hall, 1990; see also Sire *et al.*, 2009; Vickaryous & Sire, 2009) or resident populations of latent osteoprogenitors (or possibly their mesenchymal stem cell precursors; Vickaryous *et al.*, 2015). More recent hypotheses in crocodylians, where an endothelial-to-mesenchymal transition of osteoblasts has been posited, have yet to be tested in squamates (Dubansky & Dubansky, 2018).

Osteodermine deposition (when it occurs), begins with a thin layer of vitreous tissue capping the bony OD. At this early stage, osteodermine is associated with a population of fibroblast-like cells of uncertain identity. With continued growth, the number of associated cells diminishes and the accumulating tissue begins to incorporate perpendicularly radiating Sharpey's fibres (Vickaryous *et al.*, 2015).

Unusual for a skeletal element, ODs in at least some lizards are also capable of regenerating. Regenerated ODs have been reported for the anguids *A. fragilis* (Schmidt, 1914*a*; Bryant & Bellairs, 1967), *Diploglossus monotropis*, *D. plei*, *Celestus bivittatus*, *C. occiduus*, and *Ophiodes striatus* (Bochaton *et al.*, 2015), and the geckos *T. annularis* and *T. mauritanica* (Vickaryous *et al.*, 2015). OD regeneration is also predicted to occur in *Geckolepis maculata*, an OD-bearing gecko species capable of regional integumentary skin loss (Paluh *et al.*, 2017). Similar to the original elements, regenerated ODs form within the (regenerated) superficial dermis adjacent to the contact with the deep dermis. In *Tarentola*, regenerated ODs also develop a capping layer of osteodermine, which is associated with a monolayer of fibroblast-like cells (Vickaryous *et al.*, 2015). However, regenerated ODs are not identical replacements. For example, in *A. fragilis*, *T. annularis* and *T. mauritanica*, regenerated ODs differ from their original counterparts in that they are smaller and demonstrate a different overall pattern of distribution across the tail (Bryant & Bellairs, 1967; Vickaryous *et al.*, 2015). In *Diploglossus* and *C. occiduus*, regenerated ODs have a pit-like superficial ornamentation and bevelled edges not present in the original organs (Bochaton *et al.*, 2015). As a result of these additional articulations, the regenerated tail is reportedly less flexible than the original. Further, the histology of regenerated ODs is also different in *D. monotropis* and *C. occiduus*: whereas the largest regenerated ODs develop Sharpey-fibred bone (along the lateral margins), this tissue does not form in original ODs (Bochaton *et al.*, 2015).

(3) Osteoderm development in other amniotes

Outside of lizards, OD development has been investigated in the crocodylians *Caiman crocodilus* (Schmidt, 1914*b*) and *Alligator mississippiensis* (Vickaryous & Hall, 2008; Dubansky & Dubansky, 2018) and the armadillo *Dasypus novemcinctus* (Vickaryous & Hall, 2006). As in lizards, OD formation in both these taxa occurs within well-differentiated dermis, asynchronously across the body. Although OD formation is relatively delayed compared with most of the skeleton, it does vary: in crocodylians, ODs develop 9–12 months after hatching (Vickaryous & Hall, 2008; Dubansky & Dubansky, 2018), while in armadillos they first appear in the late-stage fetus (Vickaryous & Hall, 2006). Whereas OD development in crocodylians has been reported to occur *via* direct osseous metaplasia in mainly paravertebral ODs (Vickaryous & Hall, 2008), emerging evidence from nuchal ODs points towards intramembranous ossification (Dubansky & Dubansky, 2018). While this may partially reflect the difference in underlying soft tissue architecture with the paravertebral ODs co-opted for bracing (Salisbury & Frey, 2001), the more recent study by Dubansky & Dubansky (2018) found that while OD development initially involved the formation of a fibrous concentration within the dermis, this primordium was soon populated by an aggregation of mesenchymal and osteoblastic cells. With continued growth, osteoid is deposited and mineralised to yield bone. Intriguingly, the authors found that some of the osteoblasts associated with osteoid expressed the endothelial marker TIE-1 (tyrosine kinase with immunoglobulin-like and EGF-like domains-1). By way of explanation, it was proposed that at least some of the osteoprogenitors contributing to OD formation are derived from endothelial cell populations, raising the possibility of an endothelial-to-mesenchymal transition (Dubansky & Dubansky, 2018). In this scenario, endothelial cells from small-calibre blood vessels separate from the existing vasculature, become mesenchymal and then migrate towards presumptive ODs. Once invested in the presumptive OD, these mesenchymal cells differentiate into osteoblasts and contribute to the formation of osteogenic cell condensations (Dubansky & Dubansky, 2018). Armadillo ODs also develop from a condensation of osteoblasts *via* intramembranous ossification (Vickaryous & Hall, 2006). However, the role (if any) of endothelial cells in the osteogenic population remains unknown. It is also worth noting that unlike some lizards, ODs in crocodylians and armadillos do not regenerate (Pressinotti *et al.*, 2013; see also Vickaryous *et al.*, 2015).

(4) Future targets

As noted above, many aspects of OD development are poorly understood. In lizards, some of the key questions include:

what is/are the cellular origin(s) of the osteoblasts involved in OD development? Which cell type is responsible for osteodermine/capping tissue deposition? Does the epidermis participate? Is there a role for endothelial-to-mesenchymal transition in lizard ODs? To understand better the developmental mechanisms underlying OD formation in lizards, future studies will need first to dissect cellular behaviours of the relevant cell populations including proliferation and differentiation, using histological markers and gene expression studies. Such step-by-step analyses sampling both phylogenetic diversity and multiple developmental stages hold promise to uncover the basic principles of OD biogenesis from the perspective of cellular events. Comparative analyses of ODs of different shape and structure aimed at investigating cell behaviour during their development will help determine how alterations in cellular biology affect OD morphogenesis in different species. Once morphogenesis is understood at the cellular level, we can begin to explain how OD shape diversity and distribution pattern are generated by changes in the underlying molecular and genetic processes.

Specific molecular targets for analysis of lizard OD development can be drawn from the literature on other species forming mineralised dermal structures, and their relationship with epidermal elements such as the chelonian carapace and plastron, and crocodilian ODs. Intratendinous metaplasia (the transition from mature dense connective tissue to mineralised tissue), as described above for lizards, is also found in portions of other reptilian and dinosaur ODs and turtle shells (see also Scheyer & Sander, 2004; Scheyer, 2007; Horner, Woodward & Bailleul, 2016). In the formation of turtle shells intramembranous ossification is associated with the sequential and overlapping Hedgehog and canonical Wnt (segment polarity pathway *wingless*' vertebrate homolog) signalling which are proposed to direct osteochondrogenic cells to choose an osteogenic path and prevent them from transdifferentiating into chondrocytes (Rice *et al.*, 2016). Additionally, similar to alligator ODs, ossification centres in the dermis are seen in the plastron and carapace of the turtle shell (Cherepanov, 1997; Cebra-Thomas *et al.*, 2005, 2007; Vickaryous & Hall, 2008; Hirasawa, Nagashima & Kuratani, 2013). These findings suggest testable predictions and provide a platform allowing further dissection of OD development in lizards at the cellular, molecular and genetic levels.

Additional molecular targets may be derived from the literature on odontoblasts and cranial dermal bone osteoblasts, the cells responsible for bone and dentine formation which are derived from neural crest mesenchymal cells (Sire & Kawasaki, 2012). Their differentiation and resulting tissue morphogenesis are known to be regulated by skeletogenic signalling molecules and transcription factors. Mesenchymal (possibly neural crest cell-derived) condensations give rise to skeletogenic cells, such as scleroblasts, and are also thought to be involved in synthesis of type-I collagen and acidic secretory calcium-binding phosphoproteins (SCPPs) (Kawasaki, Suzuki & Weiss, 2004). These acidic SCPPs are encoded by the gene *SPARCL1* and help regulate crystallisation of calcium phosphate-based mineral in bone and dentine in vertebrates. SCPPs have been identified in the genomes of humans, lizards, chickens, frogs and zebrafish (*Danio rerio*). Specifically, dentine sialophosphoprotein 1 and 2 (DSPP1, DSPP2), dentine matrix acidic phosphoprotein 1 (DMP1), integrin-binding sialoprotein (IBSP), matrix extracellular phosphoglycoprotein (MEPE) and secreted phosphoprotein 1 (SPP1) have been identified on chromosome 8 in lizards (Sire & Kawasaki, 2012). Thus, future studies will need to investigate expression patterns of multiple developmental genes and their combinations to define more precisely relevant developmental processes and to distinguish among various alternative interpretations.

V. BIOMECHANICS, BIOMIMETICS AND BIOINSPIRATIONS

(1) Biomechanics

Classical engineering methods and techniques are promising tools to advance our fundamental understanding of the selective advantages of different OD morphologies and arrangements from a biomechanical point of view. Material characterisation using compressive or tensile forces applied to a single or sheets of ODs enables us to estimate their inherent mechanical properties. On the other hand, computational modelling techniques such as finite element (FE) methods are powerful tools allowing us to model ODs virtually, and to alter their structure and morphologies in hypothetical scenarios to understand possible correlations between their structure, form, and function (Fig. 5).

A relatively large body of research has characterised the mechanical properties of fish scales (e.g. Song, Ortiz & Boyce, 2011; Allison *et al.*, 2013; Yang *et al.*, 2013, 2014; Ebenstein *et al.*, 2015; Arola *et al.*, 2018) and ODs in a range of tetrapod species (Chen *et al.*, 2011; Rhee, Horstemeyer & Ramsay, 2011; Damiens *et al.*, 2012; Chen, Yang & Meyers, 2014, 2015) but very few studies have applied these techniques to lizard ODs (Broeckhoven *et al.*, 2015, 2017*a*, 2017*b*; Iacoviello *et al.*, 2020). This is unfortunate given that lizards show the greatest diversity in OD macro- and microstructure of any tetrapod group. Table 2 summarises the range of mechanical properties that have been measured in ODs in only three studies in lizards. These data show a large variability in results for the same species. This could be due to the implemented technique, the treatment of the sample before characterisation, or the anatomical region from which the sample was collected.

Given that ODs are not homogenous, variation would be expected in the inherent mechanical properties of different regions of a single OD. The study of Iacoviello *et al.* (2020) is, to the best of our knowledge, the only example highlighting the variation in the mechanical properties of tissues within a single OD in *Heloderma* (Fig. 5A–C). They found that the capping tissue (osteodermine) had the highest elastic modulus (*ca.* 20 GPa), followed by a mineralised region

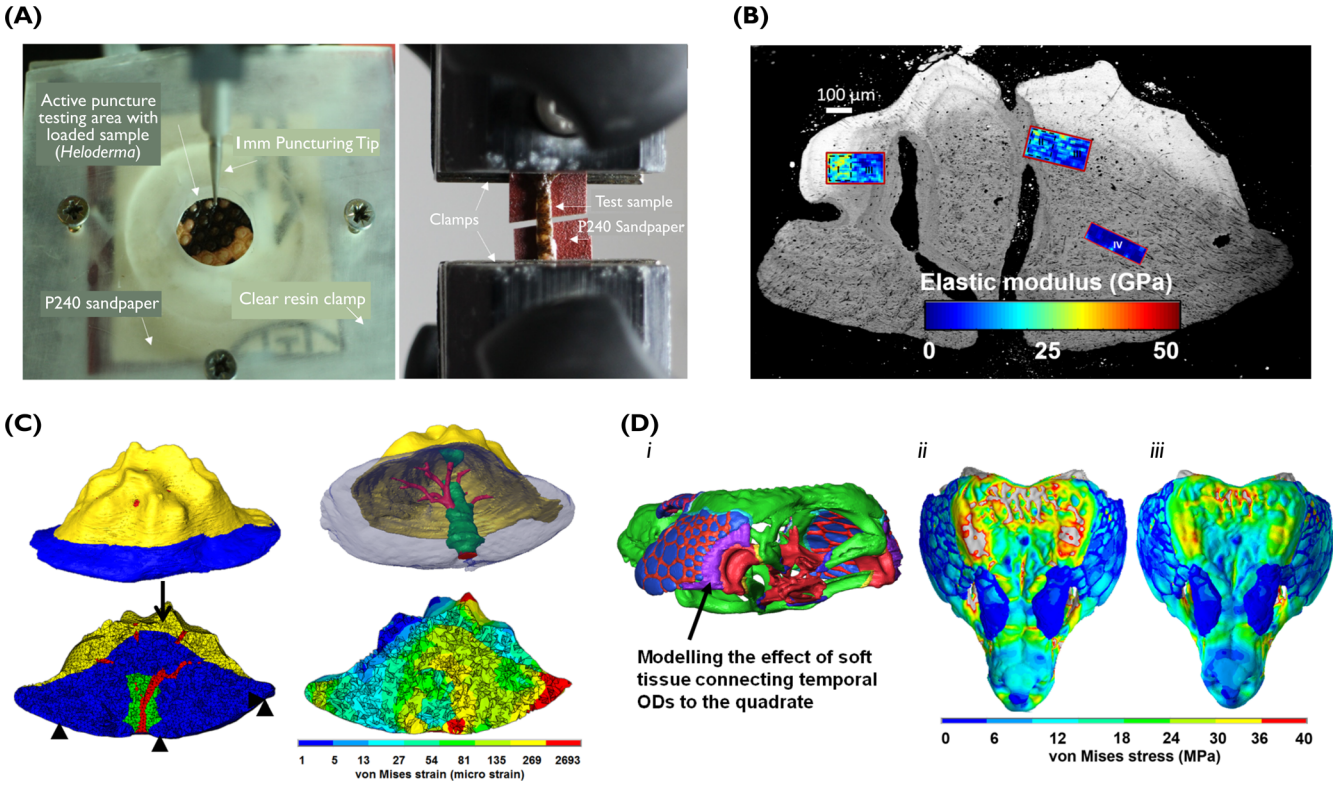

Fig. 5. Biomechanical characterisation of *Heloderma suspectum* osteoderm (OD). (A) Illustration of material characterisation (tensile and puncture testing) of sheets of skin (unpublished data). (B) Atomic force microscopy of a single OD. (C) Finite element simulation of a single OD under compression (adopted and modified from Iacoviello *et al.*, 2020). (D) (*i*) Three-dimensional reconstruction of the skull of the lizard *Timon lepida*; green, cranial bone; blue, free ODs; purple, temporal-ODs and quadrate attachment. (*ii*, *iii*) Modelling anterior biting. Von Mises stress due to bilateral bite of 170 N (based on published data), with temporal ODs not connected (*ii*) or connected (*iii*) to the quadrate.

displaying cells and a bone-like morphology (surrounding the blood vessel channels in the OD; *ca.* 10 GPa), and then by a relatively softer deep region composed of cells with regularly interspaced fibre bundles that weave into a mineralised matrix (*ca.* 3 GPa). Considering sheets of ODs, given the morphological variations within and among species, it is likely that the overall stiffness and toughness of ODs could vary and that they would deform differently depending on the way that they are loaded (mimicking different predators; Broeckhoven *et al.*, 2015, 2017*b*). In this respect, more work needs to be carried out across a wider range of lizards to map out the mechanical properties of ODs and to correlate their properties to other factors, such as their macroscopic structure and ecological differences.

A number of other studies have used the FE method to investigate the role and function of ODs in a range of tetrapod species (Rivera & Stayton, 2011; du Plessis *et al.*, 2018). However, very few studies have applied this technique to lizard ODs (Clarac *et al.*, 2017, 2019; Iacoviello *et al.*, 2020). From a thermal perspective, the FE results of Clarac *et al.* (2017) suggested that although the mineralised parts of ODs may not themselves play a role in cutaneous heat conduction, the network of blood vessels within the ODs could contribute to heat exchange between the lizard and its environment. From a structural perspective, it seems that, depending on how loosely or rigidly ODs are attached to the skeleton, they may contribute to the overall loading that the skeleton undertakes (Fig. 5D; Xue *et al.*, 2017). On the other hand, ODs may be optimised and adapted to the mechanical environment that they experience. The FE studies of Clarac *et al.* (2019) suggested that the dorsal keel on crocodylomorph ODs might play a role in reducing the overall stress across the OD. Similarly, the FE studies of Iacoviello *et al.* (2020) suggested that the structural heterogeneity within a single OD could represent an adaptation to enhance its resistance to the external load. Nonetheless, given the morphological and structural diversity of lizard ODs, further work in a wider range of species is needed to describe the biomechanical spectrum of these structures.

(2) Biomimetics and bioinspiration

Despite a relatively large body of research on the development of biomimetic and bioinspired structures, based on what we know from fish scales [e.g. Chintapalli *et al.*, 2014; Rudykh, Ortiz & Boyce, 2015; Martini, Balit &

Table 2. Summary of mechanical testing carried out on lizard osteoderms (ODs) and comparison species, to quantify their elastic modulus and load to failure under puncture testing. *Compression puncture test was carried out using the upper jaw of various mongoose species and load to failure (unit N) was reported.

Specimen	E (GPa)	Testing method	Reference
Turtle shell			
Terrapene carolinensis	18.3–24.8	Nanoindentation	Rhee *et al.* (2009)
Chelydra serpentina	0.5–22.1	Nanoindentation	Balani *et al.* (2011)
Terrapene carolina	0.4–1.01	Compression	Damiens *et al.* (2012)
Trachemys scripta	0.9–1.7	Compression	Zhang *et al.* (2012)
Trachemys scripta	0.7–16.5	Nanoindentation	Achrai & Wagner (2013)
Dermochelys coriacea	0.8–1.8	Compression	Chen *et al.* (2015)
Centrochelys sulcata	3.2–5.5	Nanoindentation	Jongpairojcosit & Jearanaisilawong (2017)
Armadillo	0.1– 0.4	Tensile	Chen *et al.* (2011)
Dasypus novemcinctus	1.3–4.6	Microindentation	Rhee *et al.* (2011)
Alligator	0.9–1.2	Compression	Sun & Chen (2013)
Alligator mississipiensis	1.4–20	Nanoindentation	
	2.2–5.7	Compression	Chen *et al.* (2014)
Cordylidae*			
Ouroborus cataphractus	63.7–79.5 (N)		
Karusasaurus polyzonus	18.7–25.6 (N)	Compression on sheet of ODs	Broeckhoven *et al.* (2015)
Namazonurus peersi	14.4–19.0 (N)		
Cordylus macropholis	18.7–27.0 (N)		
Cordylus cordylus	14.8–21.9 (N)		
Cordylidae			
*Ouroborus** *cataphractus*	75.7 ± 23.5 (N)	Compression	Broeckhoven *et al.* (2017*b*)
*Smaug** *giganteus*	110.4 ± 12.4 (N)		
Heloderma suspectum	2.7–19.1	Atomic force microscopy on single OD	Iacoviello *et al.* (2020)

Barthelat, 2017; see also Connors *et al.*, 2019 on chiton scales] and ODs from a range of tetrapod species (see review by Yang *et al.*, 2013), to the best of our knowledge no study has used lizard ODs as a model system. The existing literature in this area has highlighted the potential applications of scales/ODs and the concept of tessellation, for body armour with increased fracture resistance (Fratzl *et al.*, 2016; Naleway *et al.*, 2016). However, our understanding of the effect of different OD morphologies in enhancing, for example, the fracture resistance or shock absorption capacity of body armour is still limited. Building on a greater knowledge of lizard OD patterning and morphology, future studies can use advanced computational and experimental techniques to characterise the biomechanics of ODs in different lizards. Such studies can naturally set the foundation for future biomimetic and bioinspiration research focused on lizard ODs.

VI. FUNCTION

The formation of skeletal elements within the skin has high costs in terms of nutrients and energy (Giles, 1983; Spence, 2012), therefore OD function must warrant these costs. In tetrapods generally, ODs are most commonly hypothesised to function as defensive armour, whether against predators, conspecifics, or aggressive prey (Moss, 1972; Seidel, 1979; Albertson *et al.*, 2009; Vickaryous & Sire, 2009; Hayashi *et al.*, 2010; Yang *et al.*, 2012; Vickaryous *et al.*, 2015; Broeckhoven *et al.*, 2018*a*; Laver *et al.*, 2020), so much so that the terms 'osteoderms' and 'armour' are sometimes used as synonyms (Yang *et al.*, 2012; Laver *et al.*, 2020). Among lizards, only the OD-rich skin of five cordylid species has been tested for its toughness (Broeckhoven *et al.*, 2015). Skin toughness was found to be correlated with OD coverage and thickness but not with the thickness of the epidermal armour (i.e. β-keratin). However, with the exception of *Ouroborus cataphractus*, which could withstand simulated bites from several mongoose species, the skin of those lizards tested failed to endure the simulated bites of their mammalian predators. The early diversification of ODs in cordylids was suggested to be coupled with rapid defensive trait diversification (Broeckhoven *et al.*, 2016). However, that diversification of defensive traits appeared unrelated to predation risk associated with microhabitat use (Broeckhoven *et al.*, 2016, 2018*a*). Therefore, although the primary role of ODs is likely to reinforce the structural rigidity and mechanical toughness of the skin, it would be simplistic to imply that this is their only function.

Several additional or alternative hypotheses of OD function have been proposed across tetrapods, including thermoregulation due to their vascularisation (Seidel, 1979; de Buffrénil *et al.*, 1986; Farlow, Hayashi & Tattersall, 2010; Hayashi *et al.*, 2010; Broeckhoven *et al.*, 2015, 2017*b*; Clarac *et al.*, 2017, 2020; see Section V.1), structural support of the vertebral column (Frey, 1988; Losos *et al.*, 2002; Buchwitz *et al.*, 2012), social display/recognition (Main *et al.*, 2005; Hayashi *et al.*, 2010; Saitta, 2015), metabolic or mineral

regulation, lactate sequestration, and calcium reserve (Moss, 1972; Seidel, 1979; Jackson, Andrade & Abe, 2003; Marinho, 2007; Warren & Jackson, 2008; Farlow *et al.*, 2010; Janis *et al.*, 2012; Dacke *et al.*, 2015; Paluh *et al.*, 2017; Vidal *et al.*, 2017), water retention (Khalil & Abdel-Messeih, 1962; Witzmann, 2009), as exoskeletal attachment for tendons (Seidel, 1979), or as camouflage (Albertson *et al.*, 2009; Schucht *et al.*, 2020). Yet, to date, many of these hypotheses remain untested, and for those that have (e.g. lactate sequestration, locomotor support, thermoregulation), the work has mainly focused on crocodiles or turtles, rather than terrestrial squamates.

In squamates, Camp (1923) associated the absence of OD expression (e.g. in amphisbaenians, dibamids) with burrowing. Coe & Kunkel (1906) similarly observed that the ODs of the Anniellidae (Anguimorpha) are greatly reduced, apparently by vacuolisation, and concluded that this was due to their subterranean life. However, caecilians (Amphibia) burrow and have skeletal elements within their skin, albeit with a potentially more flexible structure (Zylberberg & Wake, 1990). ODs have also been suggested to reduce flexibility during locomotion (Losos *et al.*, 2002), offering an alternative/additional hypothesis for their loss or reduction in long-bodied limb-reduced squamates, but many elongated anguids (e.g. *Ophisaurus*, *Anguis*) retain an extensive covering of ODs apparently without compromising their mobility. Moreover, there is a substantial OD cover in fossorial scincids and *Heloderma*, also a habitual burrow-dweller (Rieppel, 1981; Miralles *et al.*, 2015; Iacoviello *et al.*, 2020; Kirby *et al.*, 2020), albeit one that is fully limbed.

The observation that the X-ray density of ODs in *Alligator* spp. was greater in females with ripe ovarian follicles compared to those that had recently laid eggs (Dacke *et al.*, 2015) led to the suggestion that lizard ODs may sometimes play a role in calcium storage (Paluh *et al.*, 2017). However, Laver *et al.* (2020) argued that the enlarged calcium-dense endolymphatic sacs in the small number of OD-bearing gekkotans (*Gekko gecko*, *G. reevesii*, *Geckolepis* spp., *Tarentola* spp.), in comparison with the majority of OD-less species, were evidence that, at least in gekkotans, ODs are structures that require rather than provide calcium resources, their importance being in other roles, notably in reinforcement of the skin.

Cordylids and their sister group gerrhosaurids form a small clade of scincoid lizards from sub-Saharan Africa that show striking variation in OD coverage from a full-body covering (e.g. *Broadleysaurus*) to almost complete absence (e.g. *Platysaurus*) (Stanley, 2013, 2016; Broeckhoven *et al.*, 2015, 2017*a*, 2017*b*; Broeckhoven *et al.*, 2018*a*). This renders cordylids an interesting study group in which to explore OD function. This series of papers emphasised the multi-functionality of ODs (e.g. protection *versus* thermoregulation, as high vascularity may weaken ODs; Broeckhoven *et al.*, 2017*b*), and the possible trade-offs between these different roles (Losos *et al.*, 2002). They found that ODs could be sexually dimorphic (Broeckhoven *et al.*, 2017*a*), developing on the trunks of male lizards around the time of sexual maturity when agonistic intraspecific encounters occur where males bite each other's bodies. In this case, the role of ODs is likely protective.

Thus, the presence, absence, and degree of OD cover for individual species (or individual animals within each species) likely depends on the interplay of, and trade-offs between, a combination of factors, including environmental factors (e.g. aridity *versus* humidity, prevalence of shelter and ground cover), the likelihood and type of predator encounters, the ability to capture agile prey, and the danger from conspecific agonists or aggressive prey (Broeckhoven *et al.*, 2015, 2017*a*; Broeckhoven *et al.*, 2018*a*; Broeckhoven, Le Fras Nortier Mouton & Hui, 2018*b*). The selective pressures on ODs expressed in different anatomical regions may also vary, leading to differential regional expression, for example in the cranium (Lacertididae) or the tail [*Platysaurus* (Cordylidae)] while lost elsewhere.

While lizard natural 'body armour' might serve as bioinspiration for the development of artificial protective materials, it would be important to focus on those species in which ODs serve a likely protective function, whether from predators or conspecific aggression, although other functions cannot be excluded. Therefore, data on the function(s) of ODs are important for reverse engineered applications.

VII. CONCLUSIONS

(1) The ability to express integumentary mineralisations is a trait common to vertebrates and is almost certainly an ancestral trait.
(2) Osteoderms (or their homologues) were present in the earliest tetrapods and have been lost or retained across different tetrapod lineages from amphibians through reptiles and into mammals.
(3) There is no single function that can be ascribed to osteoderms. When present, they may be protective, but there will be trade-offs in terms of skin permeability, water retention, body mass, flexibility, and calcium costs. However, hypotheses of function remain rarely tested, and purported trade-offs need to be re-evaluated in the light of a proper examination of the phylogenetic history of the clade and detailed information on the ecology of the species under study. Very little is currently known of the biomechanical properties of squamate osteoderms.
(4) Osteoderms do not seem to have been expressed in stem-lepidosaurs, perhaps reflecting their generally small size, and are found in only one extinct representative of Rhynchocephalia. They are, however, common in lizards and have been found in fossil squamates dating back to at least the Middle Jurassic (China).
(5) The superficial covering of hypermineralised capping tissue (osteodermine or similar) on the osteoderms of many squamates seems to be a derived trait for Squamata, although it may represent a re-activation of ancient ancestral pathways like those found in many fish.

(6) Developmental studies are needed to establish the cellular population (s) from which squamate osteoderms develop, and particularly whether there is an ectodermal component to the formation of the capping tissue.

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