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REVIEW

Review of osteoderm function and future research directions

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Abstract

Osteoderms, bone plates in the skin, are widely but discontinuously distributed across the phylogeny of tetrapods. This and their pronounced morphological disparity has inspired many hypotheses on possible osteoderm functions. Most of these have not been systematically studied or summarised based on the published disparate literature. We provide here a comprehensive overview of the current state of knowledge in this field with a focus on extant non-avian reptiles. We also discuss functions in other extant osteoderm-bearing taxa and those inferred from the fossil record. The hypotheses are categorised into protection, lifestyle and locomotion, physiology, and visual functions. A comprehensive overview of future directions in this field is provided. With this review, we hope to encourage future research to investigate the functional aspect of osteoderms. This might inspire biomimetics and shed light on the role that osteoderm expression may have played in shaping present-day biodiversity.

Introduction

One of the most consequential phases in vertebrate evolutionary history is the transition from an aquatic to a terrestrial lifestyle in early tetrapods. Conquering such a fundamentally new part of the biosphere required a large array of morphological modifications, including to the integumentary system (Clack, 2012). The integumentary system is comprised of the skin with its derivatives, and it forms the essential boundary between an organism and its external environment (Leach, 1961; Marshall, 1960; von Goethe, 1817). A commonly overlooked feature of the integument is its propensity to form mineralizations or bones (Main et al., 2005; Zylberberg & Wake, 1990). These integumentary bones are commonly referred to as osteoderms (Gadow, 1901). Their formation can result from direct metaplastic processes in the skin or through cell-mediated intramembranous ossification (Dubansky & Dubansky, 2018; Francillon-Vieillot et al., 1989; Haines & Mohuiddin, 1968; Hill, 2006; Vickaryous & Sire, 2009; Zylberberg & Castanet, 1985). A combination of both processes may be common, in which osteoderms initially form in the absence of differentiated osteoblasts via the direct transformation of the pre-existing connective tissue (de Buffrénil & Zylberberg, 2021; Vickaryous & Hall, 2008; Vickaryous & Sire, 2009). After this early metaplasia, osteoderms are subsequently remodelled through normal osteoblastic osteogenesis (de Buffrénil & Zylberberg, 2021; Dubansky & Dubansky, 2018). Different thereof, the turtle carapace is derived in large parts from endoskeletal elements in its early development (Hirasawa et al., 2013), but dermal tissue is integrated via metaplastic ossification in later stages (Scheyer et al., 2007, 2008; also supported by supplementary fig. S2B in Lyson et al., 2013). However, in many respects, the underlying ontogenetic and developmental processes deserve further investigation (Vickaryous & Sire, 2009).

In the existing body of literature, there seems to be no unambiguous consensus as to which structures qualify as osteoderms (and which do not). They are defined as superficial dermal ossifications that form part of the tetrapod integumentary skeleton (Francillon-Vieillot et al., 1989; Romer, 1956; Vickaryous & Sire, 2009). Structures such as postorbitofrontal, parafrontal and supraorbital bones form in deeper layers but may have been mistaken for osteoderms in the past (Bauer & Russell, 1989; Boulenger, 1887; Camp, 1923; Campbell, 1974; Gauthier et al., 2012; Griffing et al., 2018). Other contentious cases comprise mineralized scale hinges and osteoderms that are devoid of actual bone tissue (Gauthier et al., 2012; Vickaryous et al., 2022). Our understanding is further complicated by the lack of a consistent and comprehensive catalogue of osteoderm expression on a lower taxonomic level, which renders systematic investigations difficult.

Osteoderms are widely but discontinuously distributed across tetrapod phylogeny, and they exhibit a pronounced morphological disparity. This has inspired many hypotheses on possible osteoderm functions over the course of the past 170 years. These hypotheses can be broadly categorized into protection, lifestyle and locomotion, physiology and visual functions (Fig. 1). Many of the hypotheses have not been systematically studied or summarized based on the published disparate literature. We provide here a comprehensive overview of the current state of knowledge in this field based on data on extant non-avian reptiles. We complement this with data on other extant osteoderm-bearing taxa. For the extinct groups, we discuss functions that have been inferred from the fossil record. This can be done with a certain degree of confidence through comparative approaches and extant phylogenetic bracketing (Witmer, 1995). With this review, we hope to encourage future research to investigate the functional aspect of osteoderms in extant taxa. This can be of interest as a basis for new biomimetic materials (e.g. Yang et al., 2013), but also shed light on the role that osteoderms may have played in the past and what impact they may have had on shaping present-day biodiversity.

Osteoderm origins, occurrence and structure

Bony dermal scales (not to be confused with epidermal keratin scales) are virtually ubiquitous in 'fish'. Why then do vertebrate osteoderms require separate consideration? The origins of the integumentary skeleton can be traced back to the exoskeletons of Ordovician agnathans (Denison, 1968; Janvier, 2015; Sansom et al., 2005; Sire et al., 2009) and the rhombic scales found in the stem-Osteichthyes (Vickaryous & Sire, 2009). In the Devonian, early stem-tetrapods such as *Acanthostega* and *Ichthyostega* retained many piscine features, including a ventral covering of comparatively thin scales (Janvier, 1996; Romer, 1956). Thus, dermal scales clearly predate osteoderms (Sanchez et al., 2021). They were retained in some early tetrapods but lost in most crown lineages (Mondéjar-Fernández et al., 2014; Mondéjar-Fernández & Janvier, 2021). As an exception, they persisted in temnospondyls and, till present day, in caecilians – albeit in a structurally simplified form (Mondéjar-Fernández & Janvier, 2021; Witzmann, 2011; Zylberberg et al., 1980). In addition to scales, several temnospondyls evolved osteoderms with different microstructural organizations and developmental origins, suggesting convergent evolutionary pathways (de Buffrénil et al., 2016; Sanchez et al., 2021; Witzmann & Soler-Gijón, 2010). Nonetheless, a deep homology may underlie the repeated acquisition of osteoderms in tetrapods, in which the integument expresses an (often latent) structural propensity to form mineralizations or bones (Hill, 2006; Main et al., 2005; Vickaryous & Hall, 2008; Zylberberg & Wake, 1990). Therefore, both dermal scales and osteoderms may be considered structurally derived forms of an ancestral feature.

From a developmental perspective, the elasmoid scales found in most bony fish are of mesodermal origin (Mongera & Nüsslein-Volhard, 2013). However, they represent a highly derived scale type (Mongera & Nüsslein-Volhard, 2013). In early-diverging lineages of bony fishes, neural crest cells give rise to the osteoblasts of the scales, as exemplified in sturgeon (Stundl et al., 2023; Tew, 2023). It can be argued that this may be the ancestral state. Likewise, tetrapod osteoderms are hypothesized to develop from neural crest cells (Krmpotic et al., 2021; Moss, 1969; Sire et al., 2009; Smith & Hall, 1990; Vickaryous & Sire, 2009). However, experimental data remains

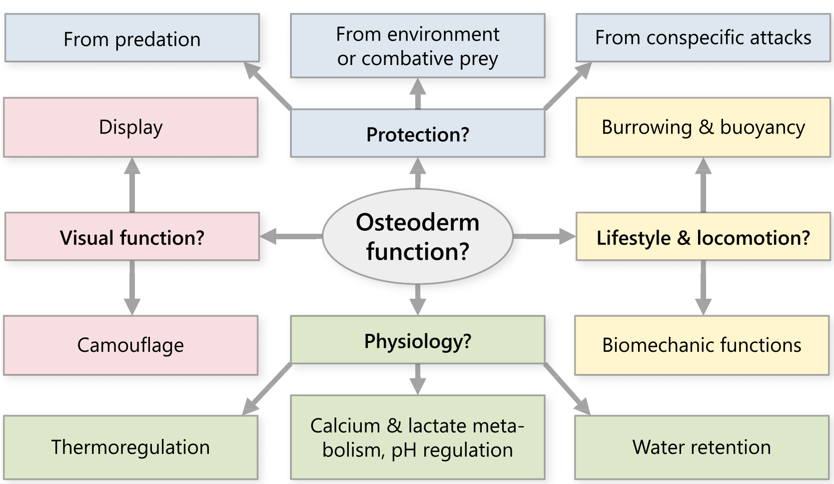

Figure 1 Schematic overview of proposed osteoderm functions. For references, see text chapters.

limited (e.g. Cebra-Thomas et al., 2013; Clark et al., 2001; Gilbert et al., 2007; Goldberg et al., 2020). Moreover, developmental mechanisms may not be uniform throughout the tetrapod tree of life. This has been demonstrated in *Alligator mississippiensis*, whose osteoderms are formed from mesodermal tissue (Dubansky & Dubansky, 2018). Ultimately, the developmental origin of tetrapod osteoderms and 'fish' scales remains to be fully understood, and neither ontogeny nor evolutionary history appear to provide a clear and reasonable distinction between these structures. Given that tetrapods are nested within vertebrates, it may be necessary to think of osteoderms as a subcategory or derivative of dermal scales *sensu lato*.

After most crown-tetrapods lost their dermal scales, sturdier osteoderms became the dominant integumentary mineralizations (Sanchez et al., 2021; Vickaryous & Sire, 2009; Witzmann & Soler-Gijón, 2010). Osteoderms consolidated the dense integument of Carboniferous tetrapods, such as the Temnospondyli (Witzmann, 2009). This may have provided a better resistance against water loss and mechanical damage such as abrasion during locomotion on land (Witzmann, 2009). In early Permian amphibians, such as *Cacops* and *Dissorophus*, osteoderms may not only have provided protection from water loss, but also facilitated terrestrial locomotion by strengthening the vertebral column (Berman et al., 1985; Coldiron, 1974; DeMar, 1966, 1968). Thus, osteoderms may have played a key role as a terrestrial modification in these early tetrapods.

Subsequently, osteoderms are believed to have been lost many times across different tetrapod lineages and retained in others (Williams et al., 2021). Therefore, they occur widely but inconsistently across the vertebrate phylogeny. They are found in various extant and extinct amphibian lineages (Berman et al., 1985; Coldiron, 1974; DeMar, 1966, 1968; Francillon-Vieillot et al., 1989; Leydig, 1857, 1868; Quinzio & Fabrezi, 2012; Ruibal & Shoemaker, 1984; see Fig. 2). In the extant Mammalia, osteoderms are found in armadillos (Hill, 2006; Krmpotic et al., 2015, 2021; Maden et al., 2023; Vickaryous & Hall, 2006; see Fig. 2) and in the spiny mice *Acomys* (Maden et al., 2023; Niethammer, 1975; see Fig. 2). They were also mentioned in pangolins (e.g. Janis et al., 2020). However, to our best knowledge, conclusive evidence for osteoderms in this group has yet to be presented (e.g. Kawashima et al., 2015; Wang et al., 2016). Other calcified integumentary structures in extant mammals that deserve further investigation include the tubercles found in the skin of porpoises (Behrmann, 1996; Burmeister, 1869; Ginter et al., 2011; Kükenthal, 1889). In the extinct Mammalia, osteoderms occur in xenarthrans, namely in armadillos (Wolf, 2007, 2008; Wolf et al., 2012) and ground sloths (Hill, 2006), but also in representatives of cetaceans (Abel, 1901; Anonymous., 1855; Müller, 1853; von Koenigswald & Storch, 1983) and a hedgehog-like creature from the Eocene Messel pit (von Koenigswald & Storch, 1983).

Osteoderms are more common in reptiles. With the exception of birds (Hendrickx & Bell, 2021; Maden et al., 2023), they are expressed in all major archelosaurian clades, namely in crocodylians (English, 2018a; Leydig, 1857; Schmidt, 1914; see Fig. 2), turtles (Bellairs, 1970; Chen, Yang, et al., 2015; Leydig, 1857; Zangerl, 1969; see Fig. 2) and various lineages of non-avian dinosaurs (Hendrickx et al., 2022; Main et al., 2005; Vidal et al., 2017). Among extant lineages, the greatest diversity of osteoderms – in terms of shape, distribution and expression – is found in non-serpent squamate reptiles (Vickaryous & Sire, 2009; Williams et al., 2021; see Fig. 3). Only recently, osteoderms were first described in snakes, namely in sand boas of the family Erycidae (Frýdlová et al., 2023; see Fig. 3).

If extinct groups are considered, the disparity and grades of expression of osteoderms is likely largest among various Mesozoic marine reptiles. The Triassic, c. 252–200 million years ago, represents a time in Earth's history where many armoured forms inhabited aquatic habitats. These included hupesuchians (e.g. Carroll & Zhi-Ming, 1991; Chen, Motani, et al., 2015), placodont sauropterygians (Rieppel, 2000; Wang et al., 2019), saurosphargids (e.g. Li et al., 2011, 2014; Wolniewicz et al., 2023) and non-archosaurian archosauriforms (Li et al., 2016).

Also non-marine Triassic clades exhibited a spectacular osteoderm cover, such as the pseudosuchian Aetosauria and Phytosauria (de Ricqlès et al., 2021). A Triassic taxon that approached modern cordylid or egernine lizards in terms of its impressive amount of osteoderms is *Eusaurosphargis dalsassoi* (Scheyer et al., 2017), with osteoderms on the vertebrae, shoulder and ribs, ossicles along the limbs, and laterally arranged leaf-like osteoderms between the ribs and gastralia. In other taxa such as pareiasaurs from the Permian (Lee, 1997) and later in the ankylosaurian dinosaurs, osteoderm coverage could be quite extensive both on the postcranial skeleton and the cranial region, up to the development of a disk-like bony eyelid (Coombs, 1972). However, it remains unresolved if this hypertrophied palpebral is an osteoderm in the strict sense.

Osteoderms are highly polymorphic. They comprise structures as massive as stegosaur back plates, which could exceed a meter in height (Revan, 2011), minute vermiform or palmate osteoderms in annelid worm lizards that are reduced to a diameter of 50 micron (Ebel et al., 2020a), and everything in between. They may be undivided or compound – that is each osteoderm may be represented by a single unit or several smaller, fused plates (Camp, 1923; Estes et al., 1988; Greer, 2007; Hoffstetter, 1962; Otto, 1909; Schmidt, 1911). They may be arranged in an overlapping, imbricating manner or in loose association – and they can be partially fused with the underlying endoskeletal bones (Bhullar & Bell, 2008; Camp, 1923; Erickson et al., 2003; Levrat-Calviac & Zylberberg, 1986; Maisano et al., 2019; McDowell & Bogert, 1954; Smith, 1935; Vickaryous et al., 2015; Zylberberg & Castanet, 1985).

Microscopically, osteoderms are often characterized by a system of fine canals that may harbour blood vessels, nerves, adipose tissue and pigment cells (Kerbert, 1877; Kirby, 2020; Leydig, 1857, 1868; Otto, 1909; Schmidt, 1912; Smith, 1935; Strahm & Schwartz, 1977). In certain distantly related squamates, the osteoderms are capped with (possibly non-homologous) dense avascular tissue (Canei & Nonclercq, 2021; de Buffrénil et al., 2011; de Buffrénil, Sire, et al., 2010; Maliuk et al., 2024; Marghoub et al., 2022; Vickaryous et al., 2015). In other cases, the entire osteoderm may be

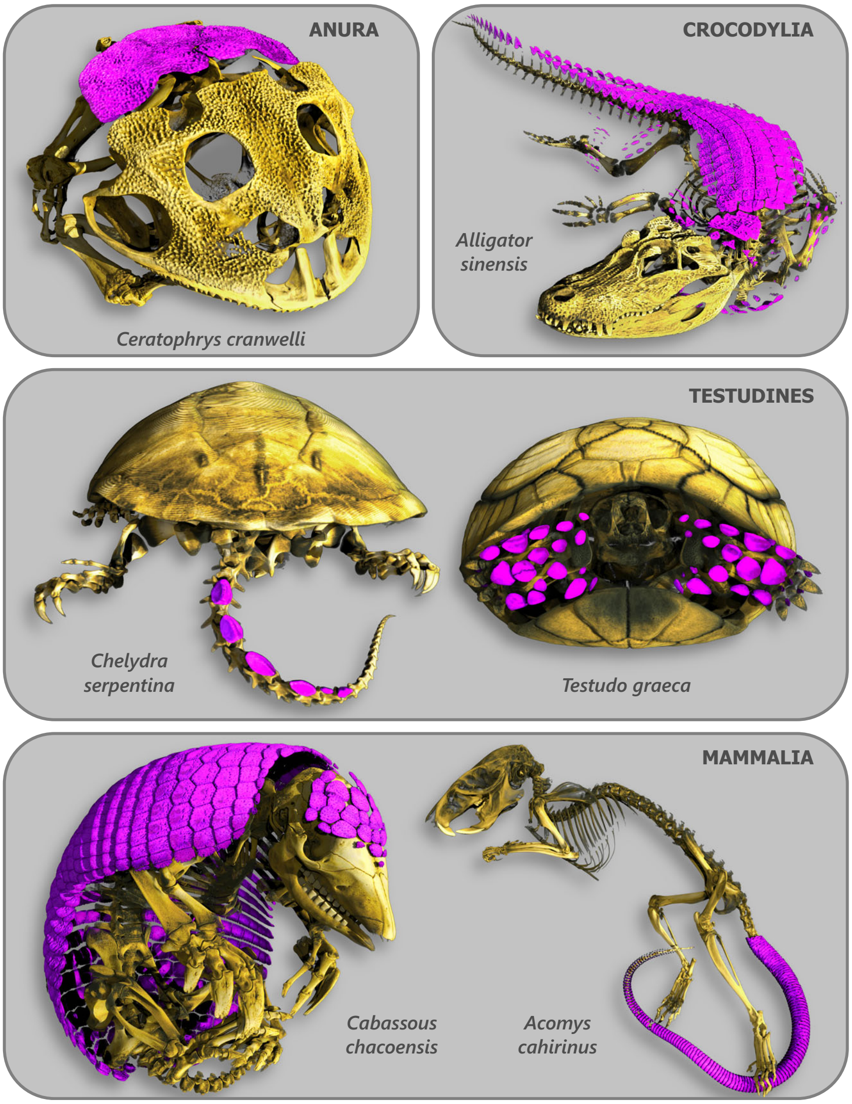

Figure 2 Examples of osteoderm-bearing taxa in non-squamate tetrapods. Volume rendering (Scatter HQ) with VGSTUDIO MAX 2024.1 (RRID: SCR_ 017997) from micro-computed tomography (μCT; Martinez & Harvard Museum of Comparative Zoology, 2019; Rockhold et al., 2019; Sridhar et al., 2018; Stanley & Yale Peabody Museum, 2018; Stanley & Yale Peabody Museum, 2019; Stanley & Florida Museum of Natural History, 2018). Osteoderms highlighted in magenta.

(nearly) avascular, such as in the geckos *Geckolepis* and *Tarentola*, the anguimorph lizard *Heloderma*, the extinct proterochampsid Archosauriformes and in certain anurans (Cerda et al., 2015; de Buffrénil & Houssaye, 2021; Levrat-Calviac, 1986; Moss, 1969; Ruibal & Shoemaker, 1984; Vickaryous et al., 2022; Willan, 2024). However, this trait is not universal to anuran osteoderms, as the vascularized osteoderms of *Beelzebufo* from the Late Cretaceous demonstrate (Evans et al., 2014). Anuran osteoderms may be co-ossified and exhibit surface sculpturing. Their numerous dermal glands are embedded in a layer of connective tissue between the osteoderms and the epidermis (Ruibal & Shoemaker, 1984). In mammals, hair follicles and glands are either embedded in bulbous osteodermal pits, such as in armadillos (Hill, 2006), or hair emerges from follicles sandwiched underneath the overlapping osteoderms, as in spiny mice (Maden et al., 2023).

Protective functions

Most intuitively, osteoderms are associated with protective functions, and they are often also referred to as dermal armour (Broeckhoven et al., 2015; Frýdlová et al., 2023). Osteoderms have been shown to distribute a locally applied load to a larger region, thus potentially decreasing damage to the underlying tissue (Yang et al., 2013). Moreover, like chain mail, their hierarchical structure with collagen fibres joining rigid units

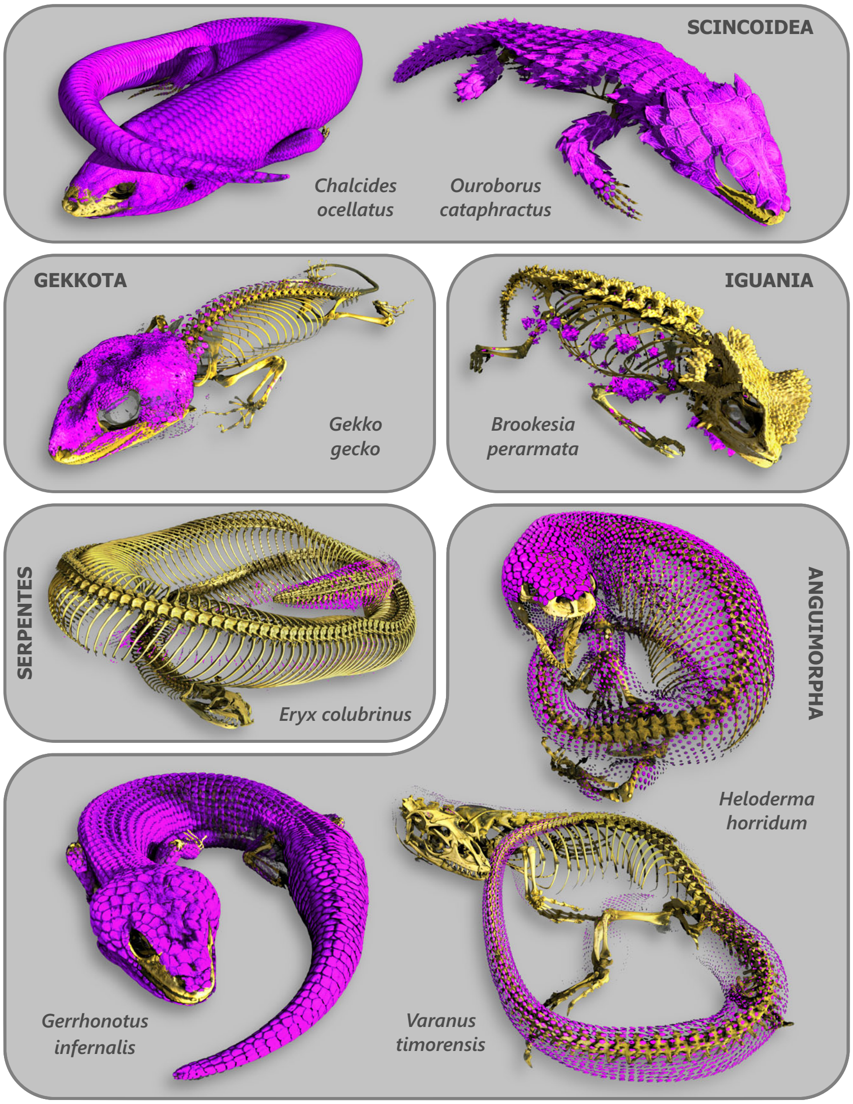

Figure 3 Examples of osteoderm-bearing squamate reptiles. Volume rendering (Scatter HQ) with VGSTUDIO MAX 2024.1 from micro-computed tomography (Anderson et al., 2018; Gray & Florida Museum of Natural History, 2023; Sibert, Gage, & Yale Peabody Museum, 2018; Stanley & Florida Museum of Natural History, 2020, 2021, 2022a, 2022b, 2022c). Limb orientation was modified in *B. perarmata* to clarify osteoderm positions. Osteoderms highlighted in magenta.

provides flexibility without significantly sacrificing strength (Yang et al., 2013). Nonetheless, robust data that could demonstrate a specific protective function of osteoderms remains surprisingly limited, and the significance of this function may be highly variable throughout ontogeny (Kirby, 2020).

Protection from predation

One of the most studied interspecific interactions is predation (Jørgensen & Fath, 2008). A possible protective function of osteoderms from predation has widely been discussed in the literature. Covered by keratinous scales, the enlarged plate- and puptent-shaped osteoderms on tortoise and extinct terrestrial turtle limbs (sometimes referred to as limb ossicles), are a good example for this. They protect the animals' more vulnerable areas on the limbs (Petrozzi et al., 2020, on *Centrochelys sulcata*), neck, and tail when completely withdrawn back into the shell (Baur, 1888; Scheyer et al., 2015; see Fig. 2).

Similarly, a protective function from predation was broadly considered for thyreophoran dinosaurs (e.g. Scheyer & Sander, 2004 and references therein). The back plates in *Stegosaurus*, however, likely provided little resistance to the bite of their typical predators (de Buffrénil et al., 1986; Main et al., 2005). The comparatively thin cortex and pronounced vascularization rather support alternative functions such as for display or thermoregulation (Farlow et al., 1976; Hayashi et al., 2010, 2012). This may also be the case for ankylosaurid osteoderms (Hayashi et al., 2010, 2012). Here, however, it has also been proposed that structural fibres strengthen the relatively brittle bone to protect it from breakage and penetration by predator teeth (Scheyer & Sander, 2004). For the sauropod titanosaurs, it has been shown that their osteoderms tend to hollow out over the course of their ontogeny, thus providing little protection from predation (Rogers & D'Emic, 2012; Silva et al., 2022). However, finite element analysis (FEA) suggests that they might have served this purpose at earlier ontogenetic stages, when osteoderms were more compact, proportionally larger and more closely arranged (Marinho, 2007; Marinho & Iori, 2011; Silva et al., 2022). In the early Permian amphibians *Cacops* and *Dissorophus*, osteoderms were long thought to provide protection against predators (Berman et al., 1985; Case, 1915; DeMar, 1968; Romer, 1947). However, more recent publications focus on a function in locomotion (e.g. Dilkes, 2009; Dilkes & Brown, 2007).

In extant tetrapods, a protective function from predation has been suggested for the osteoderms in the scincoid lizard *Ouroborus cataphractus*, which theoretically can withstand bites from several mongoose species (Broeckhoven et al., 2015). This seems to come at the cost of a reduced agility since the morphological requirements for a rapid escape and armoured defence appear to be incompatible: heavily armoured species have been found to be bulky, have short legs and run more slowly than less armoured species (Losos et al., 2002). It is noteworthy that, in many cases, ontogeny speaks against a protective function from predation. While being most vulnerable as juveniles, many taxa only express their full osteoderm cover in later developmental stages (e.g. Broeckhoven, de Kock, et al., 2017; de Queiroz, 1987; Vickaryous & Hall, 2008).

In scincid lizards, osteoderms form a coat of overlapping bone over the entire body, making their skin hard, impervious and difficult to hold (Greer, 2007; Robertson & Coventry, 2019; Shine, 1991). While not providing much protection against larger predators, their osteoderm cover may still protect them from piercing structures such as invertebrate chelicerae and vertebrate teeth (Greer, 2007). In particular, the co-occurrence of such dermal armour with the presence of venomous predators has been discussed (Youngman et al., 2021). Accordingly, snakes such as *Pseudonaja* may have co-evolved short and stiff fangs for the penetration of scincid intra-osteodermal spaces (Fry, 2015). This may be true in comparison with the long, flexible fangs of *Oxyuranus*, which are best suited for penetrating mammalian fur (Fry, 2015). However, further study is required to explore if this pattern is consistent in the Elapidae as a whole. Skinks are just one of their typical prey items and short fangs are found in various elapid taxa (Berkovitz & Shellis, 2017; Watharow, 2011).

Another modification in response to osteoderm-reinforced prey may be the hinged or jointed teeth that occur in other skink-eating snakes (Greer, 2007; Savitzky, 1981; Shine, 1991; Watson, 1993), such as *Scaphiodontophis* and *Sibynophis* (Savitzky, 1981; Vitt & Caldwell, 2014), and convergently in the ecologically equivalent pygopodid gekkotan *Lialis* (Patchell & Shine, 1986; Pianka & Vitt, 2003). It has been proposed that, when a tooth hits an osteoderm, it folds and thus allows other teeth to penetrate between scales and obtain a firm grip on the prey (Pianka & Vitt, 2003). This mechanism has been suggested to prevent tooth breakage in the process of predation (Savitzky, 1981).

Beyond load distribution and protection from penetration, osteoderms can reinforce spikes and keels that deter predators or complicate prey removal from a burrow (e.g. Chapple, 2003; Maliuk et al., 2024; Stanley et al., 2016). A special case of an anti-predator strategy is phragmosis, the closing of a burrow by means of modified body parts (Wheeler, 1927). Outside of amniotes, it is encountered in various unrelated taxa such as ants, termites, arachnids and anurans (Hölldobler & Wilson, 1990; Jared et al., 2005; Paluh et al., 2020; Schmidt, 1955; Wheeler, 1927; Wheeler & Hölldobler, 1985). Within amniotes, the osteoderm cover can support phragmotic behaviour. One such case is found in the Pygmy blue tongue skink *Tiliqua adelaidensis* (Greer, 2007). Different from other related taxa, these animals back into their tightly fitting burrows (Milne & Bull, 2000). When a predator tries to enter, the skink presents the heavy cephalic osteoderms to the intruder (Hutchinson et al., 1994). Phragmosis is also employed by the pink fairy armadillo *Chlamyphorus truncatus* while blocking the burrow entrance with its pelvic buckler osteoderms (Krmpotic et al., 2024; Schmidt, 1955). Likewise, cordylid lizards use their osteoderm-bearing tails to block access to the body while hiding in crevices (Cooper et al., 2000). In sand boas, caudal osteoderms are believed to provide protection from attacks on their exposed tail while entering burrows headfirst (Frýdlová et al., 2023). A contrasting example of a functional interaction between body armour and shelter can be found in the pancake tortoise *Malacochersus tornieri*. Their bony shell is reduced and flexible, which likely aids their unique way of wedging themselves into cracks and crevasses for shelter (Mautner et al., 2017).

Another peculiar protection strategy regards the spiny mice *Acomys*, which employ skin-shedding and tail-sheathing as a defence against predation (Maden et al., 2023). This tear-away defence might be enhanced by their caudal osteoderms (Niethammer, 1975), preventing predators from piercing through the skin and seizing the underlying unsheddable tissue (Maden et al., 2023). A similar escape mechanism, utilizing a highly fragile integument with osteoderms, has been reported for the Madagascar fish-scaled gecko, *Geckolepis* (Paluh et al., 2017). Lastly, osteoderms can also reinforce structures used as active defensive weapons, like a *Stegosaurus'* thagomizer or ankylosaurid tail clubs, with a modern analogue in *Smaug giganteus* and *Varanus acanthurus* (Arbour, 2009; Arbour & Zanno, 2020; Carpenter, 1998; Carpenter et al., 2005; Fogel, 2000; Murphy et al., 2019).

Protection from conspecific attacks

Osteoderms may also provide protection from conspecific attacks (English, 2018b). For certain species, sexual dimorphism and ontogenetic development support this hypothesis. For an example, osteoderms are expressed on the trunks of male cordylid lizard around the time of sexual maturity when agonistic intraspecific encounters occur, in which males bite each other's bodies (Broeckhoven, de Kock, et al., 2017).

Sexual dimorphism in cordylid osteoderm microanatomy might also hint at a protective function from their powerful mating bites (Broeckhoven & du Plessis, 2022; Fogel, 2003). In the gekkotan *Tarentola*, it has been proposed that the temporal sequence of their osteoderm expression reflects the typical aggressive intraspecific interactions that have been observed in high population densities, strong territoriality in the males and maternal protectivity over the clutch (Vickaryous et al., 2015). Likewise, the comparatively restricted distribution of osteoderms in *Gekko gecko*, which are mostly confined to the dorsal regions of the head and trunk, is thought to relate to their stereotypical agonistic behaviour (Vickaryous et al., 2015). Also damage patterns on osteoderms of well-preserved ankylosaur fossils were used to point at conspecific attacks (Arbour et al., 2022; Arbour & Zanno, 2020). The same might be true for large, tail club-carrying glyptodont mammals, extinct relatives of the armadillos (Alexander et al., 1999; Jusufi et al., 2023). Explicit tests of this hypothesis remain rare, however.

Other protective functions

As a special case of protection against intraspecific attacks, osteoderms have been proposed to be expressed in response to highly combative prey in the diet of certain gekkontans. For example, the skin of *Tarentola* is reinforced with an osteoderm cover, rendering it almost impenetrable to steel injection needles and thus possibly also to the sting of combative prey such as scorpions (Hoofien, 1962). A function in defence against combative prey has also been proposed for the caudal osteoderms of sand boas (Frýdlová et al., 2023). These snakes enter rodent burrows to feed on their brood, and their tail is exposed to attacks from the parent when trying to protect their litter (Hoyer, 1974).

Another often overlooked aspect of protection is that against the inanimate environment. For instance, the ventral armour in caimans is said to protect them from being injured by rocks in the fast-running streams which they inhabit (Bellairs, 1970). Ventral osteoderms, which might provide protection from abrasion, are also found in sand boas (Frýdlová et al., 2023). Likewise, abrasion resistance during belly-dragging may play a role in the osteoderm expression especially in larger, short-limbed lizards such as skinks and cordylids (in preparation).

Lifestyle and locomotion

Burrowing

Lifestyle and locomotion can be drivers for osteoderm expression (Greer, 2007). However, there is little consensus on whether or how osteoderm expression might correlate with fossoriality, that is a burrowing lifestyle (Kirby, 2020). It has been proposed that osteoderms serve as reinforcement of the skull in fossorial species (Westheide & Rieger, 2015). This is consistent with FEA results suggesting that the squamate cranial osteoderm cover relieves the underlying bone from mechanical stress (Xue et al., 2017). An opposite effect on cranial kinesis may underlie the reduction of the cranial osteoderm cover in certain rock-dwelling lacertid lizards as an adaptation to hiding in crevices (Arnold, 1973, 1998; Arnold et al., 2007).

A positive correlation with a head-first burrowing lifestyle may be supported by the occurrence of dermal mineralizations in various fossorial and semi-fossorial squamate reptiles, such as in the Anniellidae (Coe & Kunkel, 1906), the Anguidae (Kirby et al., 2020; Zylberberg & Castanet, 1985) and the Scincidae (Miralles et al., 2015; Rieppel, 1981). The latter family underwent 19 independent acquisitions of a head-first burrowing lifestyle over the past 40 million years (Ebel et al., 2020b). At the same time, scincid lizards exhibit less pronounced fossorial modifications in their skull roof structure than other head-first burrowing squamates (Ebel et al., 2020b). It thus stands to reason that their heavily co-ossified cephalic osteoderms with their skull may add to its rigidity for their head-first burrowing lifestyle (Heyer, 1972).

However, osteoderms are conspicuously reduced or absent in other highly specialized burrowing clades (Bellairs, 1970). A reduction has been reported in certain burrowing scincids (Smith, 1935) and the Anniellidae (Bhullar & Bell, 2008), and they are presumably absent in the Amphisbaenia, the Dibamidae and the Pygopodidae (Camp, 1923; Gadow, 1901). Moreover, it has been proposed that the absence of osteoderms in serpents [sic] might be indicative of their fossorial origin (Bellairs, 1970). This proposed incompatibility of a pronounced osteoderm cover with a fossorial lifestyle is thought to result from impaired flexibility (Williams et al., 2021) – a notion consistent with Losos et al. (2002), who propose that a heavy body armature makes rapid locomotion difficult due to the added mass and inflexibility.

The difficulty here is that lifestyle and locomotion are often inseparable from the respective defence and escape strategies. We might think of them as a two-dimensional continuum between (1) long-limbed sprinters in open terrain, (2) limbless litter-swimmers and burrowers and (3) short-limbed, slow moving taxa with heavy body armour (Fig. 4). It stands to reason that category [1] and [3] are mutually exclusive: Their escape and defence strategies dictate that short-limbed taxa express a heavy body armour, while it may be reduced or absent in long-limbed sprinters (Bonine & Garland, 1999; Kohlsdorf et al., 2001; Losos et al., 2002; Melville & Swain, 2000; Zamora-Camacho et al., 2014). Taxa in category [2], however, follow a different approach. Their limbs are reduced or absent, and they may or may not express an osteoderm cover (as discussed above). To some degree, they may exhibit reduced speed and flexibility (Camacho et al., 2022). However, they neither necessarily need to be fast nor heavily armoured since they tend to escape into nearby refuges, such as leaf-litter, tall grasses and burrows (Foster et al., 2015). Therefore, this part of the continuum may be much less subject to the selective pressures that render strategies [1] and [3] mutually exclusive. This possibly allows a greater disparity in osteoderm expression and explains the contrasting views on the relationship between osteoderm expression and a burrowing lifestyle. The interpretation is further hampered by the fact that fossoriality correlates with small size (e.g. Ebel et al., 2020b) while, at the

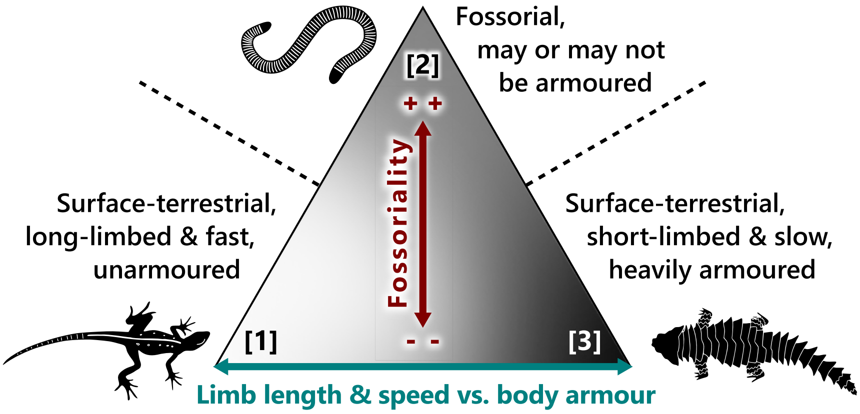

Figure 4 Hypothesized continuum between different escape strategies and osteoderm expression in squamates. [1] long-limbed sprinters in open terrain, [2] limbless litter-swimmers and burrowers and [3] short-limbed, slow moving taxa with heavy body armour. Gradient represents the absence (white) or presence (black) of osteoderms.

same time, osteoderm reduction has been attributed to miniaturization (Bhullar & Bell, 2008).

Outside of the Squamata, osteoderms have been proposed to contribute to burrowing in the early Permian amphibians *Cacops* and *Dissorophus* and in armadillos (Abel, 1912, 1919). Likewise, the rigid carapace of turtles may have initially been linked to burrowing rather than protection (Lyson et al., 2016). Caecilians, a highly derived form of fossorial amphibians, exhibit mineralized dermal scales (Williams et al., 2021; Zylberberg et al., 1980). However, these structures are more flexibly associated with the dermal tissue than is the case with osteoderms in the strict sense (Williams et al., 2021; Zylberberg & Wake, 1990), and thus provide little insight into a possible correlation between osteoderm expression and a fossorial lifestyle. Accordingly, the functional interpretation of osteoderms in burrowing taxa remains difficult.

Swimming and flight

Specific lifestyles and types of locomotion may require endoskeletal modifications. For an example, larger birds rely on their light-weight pneumatic bones for flight (Alexander, 2015). Likewise, bone compaction (osteosclerosis) and bone hyperplasy (pachyostosis) in sirens aid the passive control of buoyancy in these aquatic tetrapods (de Buffrénil, Canoville, et al., 2010). Hard tissue structure is, therefore, often diagnostic for such lifestyles (e.g. Laurin et al., 2011). It is reasonable to assume that these trends may also regard the dermal skeleton, including the osteoderms.

A pronounced osteoderm cover has been reported in presumably less agile swimmers such as the extinct teleosaurids (Hua & de Buffrénil, 1996). Other such taxa include the extinct placodonts (Rieppel, 2002; Scheyer, 2007). Here, the mass of the osteodermal shield may act as a ballast and thus facilitate the passive maintenance of their position in coastal waters (Hua & de Buffrénil, 1996; Scheyer & Sander, 2009). On the other hand, a reduction of the osteodermal shield may be attributed to the acquisition of more efficient locomotion at sea (Hua & de Buffrénil, 1996). Taxa with highly derived marine modifications, such as ichthyosaurs, plesiosaurs, metriorhynchid crocodylians (Kirby, 2020) and mosasaurs (Camp, 1923; Conrad et al., 2014) are devoid of osteoderms. A different form of aquatic modification can be found in the leatherback sea turtle. Their osteoderms form ridges along the carapace (Delfino et al., 2013; Deraniyagala et al., 1930). These are thought to enhance the hydrodynamic flow (Bang et al., 2016; Chen, Yang, et al., 2015).

Aerial locomotion comes with weight-associated constraints (Glaeser et al., 2017). It stands to reason that an osteoderm cover may be incompatible with these. Although a pronounced osteoderm cover is typical of many flightless archosaurs (Kirby, 2020), all pterosaurs, birds and possibly their extinct paravian relatives are devoid of osteoderms (Hendrickx & Bell, 2021). Consistent with this, a reduced osteoderm cover can also be found in the arboreal-gliding lacertid genus *Holaspis* (Arnold, 2002; Vanhooydonck et al., 2009), but not in their non-gliding lacertid sister-taxa *Gastropholis* and *Adolphus* (Ebel et al., 2020a; Pandelis & Long, 2018; Pyron et al., 2013).

General biomechanics

In crocodylians, osteoderms have been proposed to aid in locomotion as an exoskeletal attachment for tendons. According to Seidel (1979), the epaxial myoseptal tendons insert on the osteoderms and thus serve as an anchor in the skin to promote lateral undulations. Moreover, there are tight connections between the vertebral processes and the transverse osteoderm rows that cover the intervertebral joints (Frey, 1988a; Salisbury & Frey, 2000). This connection is relatively immobile, thus functionally turning the inter-osteodermal joints into accessory vertebral joints as part of a self-carrying bracing system, the so-called paravertebral shield (Frey, 1988b). A similar trunk bracing system may have convergently evolved in various extinct tetrapods, such as the Chroniosuchidae (Buchwitz et al., 2012) and the Dissorophidae such as *Dissorophus* *multicinctus*, and *Cacops aspidephorus* (DeMar, 1966; Dilkes, 2009; Dilkes & Brown, 2007). In the latter, vertebral lateral flexibility has been proposed to be reduced due to osteoderm fusion with the neural spines and an extensive overlap between the characteristic V-shaped osteoderms (Dilkes, 2009). Osteoderms can thus functionally be considered part of the musculoskeletal apparatus in these cases and possibly an adaptation for a terrestrial lifestyle (Coldiron, 1974; DeMar, 1966, 1968).

In other cases, osteoderms may have an opposite effect on locomotion. For instance, in scincid lizards, osteoderm thickness has been proposed to negatively correlate with their agility (Greer, 2007). Consistent with this, Losos et al. (2002) argue that a heavy body armature makes rapid locomotion difficult due to the added mass and inflexibility. Likewise, osteoderm-bearing taxa appear to invest more energy in their locomotion than non-osteoderm-bearing taxa (Farley & Emshwiller, 1996). An explanation may be that osteoderms make the skin both less flexible and heavier and, therefore, limb and body movements less efficient (Greer, 2007). It, therefore, remains difficult to provide a universal functional interpretation of osteoderm expression in the context of general locomotion.

Last, we address a non-locomotion-related aspect that has recently been identified in scincid lizards. Their cranial osteoderms have been demonstrated in FEA and *in vivo* to contribute to the biomechanics of the skull (Marghoub et al., 2023; Xue et al., 2017). By carrying load during the process of biting, strain exerted on the skull was found to be reduced by both fused or loosely attached cranial osteoderms (Marghoub et al., 2023). This entirely new aspect to osteoderm biomechanics might lead to a re-evaluation of osteoderm functions in future studies.

Physiological functions

Thermoregulation

In ecto-poïkilothermic vertebrates, the osteoderm cover may be involved in thermoregulation. For an optimal heat exchange, these animals should be equipped with a large number of superficial blood vessels controllable through dilation and constriction (Seidel, 1979). On the other hand, this condition may require some form of protection from external mechanical damage (Seidel, 1979). A cover of vascularized osteoderms meets both requirements (Seidel, 1979). Consistent with this, thermographic imaging has shown for basking caimans, crocodiles and alligators, that their osteoderms are involved in heat collection (Clarac & Quilhac, 2019; Farlow et al., 2010). The osteoderm cover has been proposed to have played a role in the crocodylian transition from endothermy to ectothermy (Clarac & Quilhac, 2019). However, more recent studies could neither detect a clear lifestyle signal in the osteoderm vascularization of crocodiles (Clarac et al., 2020), nor could they confirm significant temperature differences that relate to osteoderm expression (Inacio Veenstra & Broeckhoven, 2022). The direct contribution of osteoderms to thermoregulation thus remains a controversial topic.

Osteodermal surface ornamentation may be a modification in the context of thermoregulation (Legendre et al., 2016; Seymour et al., 2004). However, this and other micro-anatomical traits may merely co-occur with an extensive peripheral vascular network and thus not directly contribute to heat exchange (Clarac et al., 2017). Indeed, skin vascularization has been reported to be more pronounced in regions that cover osteoderms than in those without (Clarac & Quilhac, 2019). Moreover, ornamentation and a high degree of vascularization may be a natural concomitant of crocodile osteoderm physiology (Clarac et al., 2019; Farlow et al., 2010). Throughout crocodile life history, osteoderms are repeatedly remodelled (de Buffrénil, 1982) for purposes such as calcium mobilization (Dacke et al., 2015) and lactic acid buffering (Jackson et al., 2003). It is thus possible that the necessary vascularization underlying these processes may allow some degree of heat exchange (Farlow et al., 2010) without having evolved under selective pressure specifically for this function.

While all these considerations traditionally focus on radiative heat loss or gain, stegosaurs may have employed their dermal bony plates along the back and tail as counter-current heat exchangers for heat dissipation through convection (Farlow et al., 2010). These animals might have controlled the effect through input blood flow rate, shunts and body orientation with respect to the wind (Farlow et al., 2010). Seidel (1979) even proposed that stegosaur back plates may have been movably controlled by their epaxial musculature. However, histological studies have found the internal osteoderm vascularization in stegosaurs to be likely insufficient for thermoregulation (de Buffrénil et al., 1986; Main et al., 2005). Some morphological traits that can be interpreted in the context of a rich vascularization may merely be constructional artefacts that transmitted the blood supply during growth and were simply retained (Main et al., 2005). Instead, their thermoregulation might have relied on a superficial cover with highly vascularized skin (de Buffrénil et al., 1986; Farlow et al., 2010). The concept of thermoregulation through controlled blood circulation in appendages is common in amniotes (Farlow et al., 2010). Therefore, stegosaur back plates might be viewed as an equivalent to elephant ears with an accessory role in cooling (Farlow et al., 2010; Main et al., 2005). Likewise, ankylosaur osteoderm microanatomy may imply that these structures played more than just a defensive role and possibly aided in thermoregulation (Hayashi et al., 2010).

Thermoregulation has also been proposed to act as a selective pressure on the osteoderm morphology in squamates (Broeckhoven et al., 2015; Paluh et al., 2017). In scincid lizards, the osteoderms are covered with a fine reticulating system of blood vessels that can be dilated or constricted under central neurological control for thermoregulation (Drane & Webb, 1980; Greer, 2007; Hammel et al., 1967). Beyond these vessels, osteodermal canals also harbour pigment cells that might enhance heat uptake (Drane & Webb, 1980; Kerbert, 1877; Leydig, 1868; Otto, 1909). Moreover, osteoderms provide protection to the associated subcutaneous arteries (Drane & Webb, 1980). In cordylid lizards, investigations of bone microanatomy, thermal conductivity and penetration force have shown that there is a functional trade-off between protection and thermoregulation (Broeckhoven, du Plessis, & Hui, 2017). However, in contradiction to previous proposals, it appears that their osteoderm cover provides insulation against extreme temperatures due to its low thermal conductivity (Broeckhoven, du Plessis, & Hui, 2017; Broeckhoven, du Plessis, Roux, et al., 2017). Our own data confirm an according effect on passive heating and cooling rates (in preparation). Thermal insulation has also been proposed as a function for osteoderms in armadillos, which contain large cavities filled with adipose tissue (Krmpotic et al., 2015). A universal interpretation of osteoderm expression in the context of thermoregulation thus remains difficult.

Calcium metabolism

Like endoskeletal elements, the vertebrate integumentary skeleton may play a role in mineral homeostasis (Moss, 1972; Seidel, 1979). There are indications for a significant blood supply to the osteoderms over a physiologically significant time scale (Farlow et al., 2010). In crocodiles, breeding females show considerable osteoderm remodelling, accompanied by an increased plasma calcium (Kofron, 1990) and subsequent increased osteoderm porosity (Dacke et al., 2015; Tucker, 1997). This indicates that crocodylian osteoderms may act as a store for calcium that is mobilized for the formation of the egg shell (Dacke et al., 2015; Klein et al., 2009). Similarly, the highly porous and ornamented dorsal shield in dwarf crocodylians is presumed to buffer the dietary calcium deficiency that they encounter in various equatorial forest niches (Clarac et al., 2024). A function in calcium storage has also been proposed for squamates (Paluh et al., 2017). For instance, female *Ouroborus* have denser osteoderms, a trend that might be driven by reproductive needs (Broeckhoven & du Plessis, 2022). In titanosaurs, an according role may be supported by the fact that their osteoderms tend to hollow out over the course of their lifetime (Rogers & D’Emic, 2012; Vidal et al., 2017). Calcium sequestration may also have played a role in the osteoderm expression of the Triassic amphibian *Gerrothorax* to counteract episodes of osmotic stress (Witzmann & Soler-Gijón, 2010). However, this interpretation remains conjectural (Sanchez et al., 2021).

On the other hand, it has been argued that osteoderms may not provide calcium resources, but instead consume them (Laver et al., 2020; Williams et al., 2021). The authors base this on the observation that the extracranial endolymphatic sacs tend to be larger in gecko species with osteoderms than in species without them (Laver et al., 2020). These structures contain calcareous materials (Whiteside, 1922) and have thus been proposed to act as a calcium storage (Laver et al., 2020).

Lactate sequestration, pH regulation and gas exchange

Carbonate buffering (Jackson & Heisler, 1982) and lactate sequestration (Jackson, 1997) are considered important physiological functions of mineralized tissues in organisms that undergo repeated anoxic acidosis, such as turtles. From the shell, the sequestered lactate can then be shuttled back into the plasma during recovery and metabolized to increase the energetic efficiency of this process (Warren & Jackson, 2008). In caimans, which frequently face severe lactic acidosis in violent underwater struggles while overwhelming their prey, it has been shown that their osteoderms account for up to 10% of the overall buffering and sequestration capacity (Jackson et al., 2003). It has also been proposed that bone ornamentation is a result of the resorption and remodelling processes associated with buffering (de Buffrénil, 1982). The degree of bone ornamentation may thus correlate with certain lifestyles and physiologies that lead to frequent hyperkapnia and lactic acidosis (Janis et al., 2012).

A physiological constraint of pronounced dermal armour may be its disadvantage in terms of cutaneous gas exchange. This could have played a role in the osteoderm expression of some extinct dissorophoid temnospondyls, and ‘microsaur’, lysorophian and aïstopod lepospondyls (Witzmann, 2016). Also reptiles perform a part of their gas exchange through the skin (Feder & Burggren, 1985). However, this process is thought to be largely restricted to the more permeable regions of the interscalar spaces, which are devoid of osteoderms (Feder & Burggren, 1985). Historically, the pronounced vascularization in squamate osteoderms was interpreted as a network of air-filled canals and thus associated with their dermal respiration (Blanchard, 1861). However, the hypothesis has been refuted by demonstrating that these canals are filled with soft tissue (Leydig, 1868; Otto, 1909).

Water retention

It is presumed that reptilian scales and armour contribute to water retention in arid environments (Greer, 2007; Rutland et al., 2019; Witzmann, 2009). Surface evaporation through the skin has been shown to account for up to 70% of water loss in agamid lizards and geckos (Dawson et al., 1966). However, the skin in osteoderm-bearing skinks is only half as hydrated as that of squamates without an osteodermal cover (Khalil & Abdel-Messeih, 1962a), probably due to the proportionally larger amount of mineralized tissue (Greer, 2007; Khalil & Abdel-Messeih, 1962b). For example, the skink *Ctenotus labillardieri* loses only a comparatively small proportion of water cutaneously (Dawson et al., 1966). Scincid osteodermal cavities are also filled with adipose tissue (Otto, 1909), which may act as a barrier against water loss. Adipose tissue has also been found in the osteoderms of the chameleon *Brookesia* (Schucht et al., 2020) and in armadillos (Krmpotic et al., 2015). Moreover, a correlation between osteoderm expression and the aridity of the environment has been found in cordylid lizards (Broeckhoven, El Adak, et al., 2018; Broeckhoven, Mouton, et al., 2018). This qualifies water retention as one of the best-supported functions that have been proposed for squamate osteoderms. Outside of amniotes, water retention through osteoderms may have played a role in the Early Permian amphibians *Cacops* and *Dissorophus* (Berman et al., 1985; DeMar, 1966, 1968).

Other physiological functions

In addition to the bone marrow of the endoskeleton, squamates may employ tissue in their osteodermal cavities for haematopoiesis, the production of red blood cells (Kirby, 2020; Moss, 1969; Schucht et al., 2020; Weiss & Wislocki, 1956). A possible functional constraint arising from a pronounced osteoderm cover is that it may limit the ability to expand the body in the context of feeding and respiration (Leenders, 2019).

Visual functions

Osteoderms may be employed in intraspecific agonistic, deterrent or sexual display and interspecific deterrent display (Main et al., 2005). An intraspecific display function has been proposed for ankylosaurid and stegosaur osteoderms (de Buffrénil et al., 1986; Hayashi et al., 2010; Main et al., 2005). The occurrence of two discreet morphs in stegosaur back plates may support a sexual display function (Saitta, 2015). Moreover, the large plates of *Stegosaurus*, seen from a lateral view, might have made the animal appear larger to predators or rivals (Main et al., 2005). The visual effect might have also been embellished by pumping blood into the plates causing them to blush (Carpenter, 1998). However, this explanation is difficult to test and leaves those stegosaurids unconsidered that were equipped with smaller plates or only with spikes (Main et al., 2005).

Other visual functions of osteoderms may comprise ornament and camouflage (Albertson et al., 2009). Ornaments are by definition decorative rather than useful (Heacock et al., 2009). Camouflage has been discussed for chameleons, in which their spiky dorsolateral projections and osteoderms might facilitate crypsis to avoid predation (Schucht et al., 2020). However, this remains largely unexplored and there is little reason to believe that crypsis is harder to achieve with non-mineralized structures. On the other hand, chameleons exhibit bone-based fluorescence through transparent windows in their epidermis (Prötzel et al., 2018). It may thus be possible that superficially embedded osteoderms contribute to this effect in *Brookesia*, which presently is the only known chamaeleonid with osteoderms (Schucht et al., 2020). However, since the function of bone-based fluorescence remains unknown, it may rather be considered an epiphenomenon.

Future directions in osteoderm research

Firstly, we would like to note that the more recent histological findings (Vickaryous et al., 2022, 2023; Willan, 2024) may call for a clarification of the general definition of an osteoderm as a basis for future studies. Osteoderms are highly polymorphic on different structural levels, and neither ontogeny nor evolutionary history appear to provide a clear and reasonable distinction from other dermal hard tissue. We deem it possible that other terms (such as 'dermal mineralizations') may better reflect the diversity of calcified tissue that comprise the vertebrate integumentary skeleton. This would also allow us to broaden our perspective towards dermal hard tissue structures of diverse composition, organization, ontogenetic origin and evolutionary history.

For osteoderms in the traditional sense, the existing body of literature proposes a vast array of different functions. However, the majority of these have never been systematically investigated, and the functional framework, and thus the selective pressures underlying osteoderm expression, remains elusive. The current state of research implies a possible multi-functionality of osteoderms and trade-offs between different roles (Williams et al., 2021) – such as protection versus thermoregulation (Broeckhoven, du Plessis, & Hui, 2017) or a heavy armour versus rapid escape (Losos et al., 2002). Beyond this, sexual selection may be a driving factor for squamate osteoderm expression in those taxa that exhibit a pronounced sexual dimorphism (Broeckhoven, de Kock, et al., 2017). It thus stands to reason that osteoderm expression may depend on the interplay and trade-offs between a combination of these and other factors that remain to be explored (Williams et al., 2021).

By their very nature, it is difficult to study functional aspects in extinct taxa. Extant taxa that have been studied fail to fully represent the diversity of osteoderm forms and structures found in the fossil record. Of the proposed functions, lactate sequestration, locomotor support and thermoregulation have been studied most comprehensively. This work has focused on turtles and crocodylians (Williams et al., 2021), neither of which are particularly taxonomically or ecologically diverse (Bour, 2008; Martin, 2008). This limits the informative value when used as model systems for general inferences.

In crocodylians, recent studies have found osteoderm histology and ornamentation to be diagnostic for specific lifestyles, which allows functional inferences and offers a new tool for palaeoecological reconstructions (de Araújo Sena & Cubo, 2023; Pochat-Cottilloux et al., 2023). Beyond this, the thermoregulation hypothesis remains subject of ongoing discussions (Inacio Veenstra & Broeckhoven, 2022). With the mouse-like Deomyinae as an emerging mammalian model system, new light has been shed on the cellular and molecular basis of osteoderm development (Maden et al., 2023). In future studies, comparisons with reptilian osteoderms may improve our understanding of their evolution and possible constraints for their expression in mammals (Krmpotic et al., 2021; Maden et al., 2023). In the Cingulata, there have been recent advances in the use of osteoderm morphology and histology as taxonomically informative traits, both for extinct and extant representatives (Krmpotic et al., 2015; Magalhães et al., 2022; Salgado-Ahumada et al., 2023; Scarano et al., 2020). While ongoing research has started to disentangle the functional selective pressures underlying the osteoderm expression in this group, the possible impact of behavioural and morphological variations between the species remains to be studied (Krmpotic et al., 2015; Stapp, 2022).

By far the greatest diversity of osteoderms in terms of shape, distribution and expression is found in squamate reptiles (Vickaryous & Sire, 2009). Here, the most thoroughly studied group are the Cordylidae with the following findings: (1) a possible protective function from violent intraspecific behaviour is supported by evidence from the ontogeny (Broeckhoven, de Kock, et al., 2017), (2) a possible correlation of their osteoderm expression with predation pressure could only be partially be backed up with evidence (Broeckhoven et al., 2015; Broeckhoven, El Adak, et al., 2018; Broeckhoven, Mouton, et al., 2018) and 3) a correlation of their osteoderm expression with the aridity of the environment has been demonstrated (Broeckhoven, El Adak, et al., 2018; Broeckhoven, Mouton, et al., 2018).

While this research provided valuable new insight, and despite the appeal of cordylids as a model system, these findings remain to be confirmed in a broader taxonomic framework. Other functional hypotheses remain entirely anecdotal and should, therefore, be tested in future research. Where possible, effort should be made to distinguish between adaptive and secondary exaptive roles. A comprehensive overview, including our current state of knowledge and future perspectives, is presented in Table 1.

An exploration of osteoderm function *in vivo* and using museum specimens could provide additional insights into the structure~function relationships. By using strain gauges, the role of osteoderms in protective function could be studied (Kéver et al., 2022). Indeed, by measuring the deformation of the osteoderms in response to an external load, one could test the idea that thicker osteoderms deform less and provide a stiffer external surface better suited to resist external forces. Moreover, one could test the differences between compound versus single osteoderms and their role in shock absorption or load distribution. Recent studies using transducer biting have suggested that osteoderms carry load during biting (Marghoub et al., 2023), but whether this is reflected into *in vivo* behaviours such as feeding remains to be tested. In that case, cranial osteoderms might function in load distribution during the manipulation and crushing of hard objects. XROMM studies using biplanar videofluoroscopy of marked osteoderms could provide further insights into whether osteoderms structure and

Table 1 Hypothesis overview with state of research and future directions. For references, see text chapters

Functional hypothesis	What is known	Future perspectives
Osteoderms provide protection from predation	Proposed for a variety of extant and extinct taxa. Penetration force tests indicate that *Ouroborus cataphractus* osteoderms can withstand mongoose bites	Test for a correlation in an extant model system, such as squamate reptiles. Biomechanical modelling for a range of extinct and extant taxa and their typical predators
Osteoderms provide protection from conspecifics	Proposed for a variety of extant and extinct taxa. Supported by ontogeny in cordylids and the gecko *Tarentola*	Test for a correlation in a larger model system, such as squamate reptiles. Biomechanical modelling for a range of extinct and extant taxa
Osteoderms provide protection from combative prey	Proposed for the gecko *Tarentola* and sand boas	Test for a correlation in a model system, such as squamate reptiles. Biomechanical modelling for a range of taxa and their typical prey
Osteoderms provide protection from environment	Proposed for caimans and short-limbed lizards	Test for a correlation (qualitative or quantitative) between the ventral osteoderm cover and limb length in a model system, such as squamate reptiles
Osteoderms contribute to burrowing	Proposed for osteoderm-bearing head-first burrowers. Supported by FEA	Test for a correlation (qualitative or quantitative) in a model system, such as squamate reptiles. Simulate burrowing strain with and without osteoderms using validated FE models
Osteoderm impair burrowing	Proposed for non-osteoderm-bearing head-first burrowers	
Osteoderms contribute to buoyancy regulation	Proposed mostly for extinct marine reptiles, but also for the marine iguana	Test with computational buoyancy simulations
Osteoderms contribute to hydrodynamics	Confirmed for the osteodermal ridges on the carapace of leatherback sea turtles by means of flow measurements	Test in other organisms for which this may apply using 3D prints or computational models (CFD)
A pronounced osteoderm cover is incompatible with aerial locomotion	Osteoderms are absent in highly derived lineages with aerial locomotion	Test in aerodynamic simulations for extant and extinct flying taxa with and without added weight
Osteoderms are part of a self-carrying bracing system	Has been proposed for extant crocodylians and the extinct Chroniosuchidae and Dissorophidae	Test using biomechanical simulations
A heavy osteoderm cover results in slower movement	Has been demonstrated in cordylid lizards	Investigate systematically in a larger taxonomic framework, such as squamate reptiles as a whole, using an appropriate comparative framework (i.e. using phylogenetically informed analyses)
Osteoderms contribute to skull biomechanics	Has been demonstrated by FEA and *in vivo* in scincid lizards	Investigate systematically in a larger taxonomic framework, such as squamate reptiles as a whole, both during transducer biting and feeding

Table 1 Continued.

Functional hypothesis	What is known	Future perspectives
Osteoderms serve radiative thermoregulation	Has been demonstrated with thermographic imaging in crocodylians, but more recent research could not replicate this	Resolve controversy. Investigate in a larger taxonomic framework, such as squamate reptiles, using both *in vitro* (passive properties) and *in vivo* testing (role of vascular network)
Osteoderms serve convective thermoregulation	Has been proposed for stegosaur back plates	There is no extant analogue for which to test this. Simulate convective heat exchange in a model
Osteoderms serve passive thermoregulation	Thermal insulation has been proposed for armadillos, and shown for *Ouroborus* lizards in simulations, also supported by low *in vivo* cooling rates	Investigate systematically in a larger taxonomic framework, such as squamate reptiles as a whole, using *in vitro* measurements
Osteoderms serve as a calcium store	Proposed for cordylid lizards, titanosaurs and vertebrates in general. Supported by calcium shift from osteoderms to plasma in breeding female crocodiles	Investigate systematically in a larger taxonomic framework, such as squamate reptiles as a whole. Conduct experimental studies using *in vivo* μCT in females before, during and after being gravid
Osteoderms serve carbonate buffering and lactate sequestration	Inferred from observations in other hard tissues. In caimans, osteoderms were shown to account for up to 10% their buffering and sequestration capacity	Investigate systematically in a larger taxonomic framework, such as squamate reptiles as a whole
Osteoderms impact cutaneous gas exchange	Proposed for early tetrapods	Quantify cutaneous gas exchange in extant frogs with and without osteoderms
Osteoderms serve water retention in arid environments	The osteoderm-bearing skink *Ctenotus* has been shown to lose comparatively little water cutaneously. A correlation between osteoderm expression and aridity has been found in cordylid lizards	Investigate systematically in a larger taxonomic framework, such as squamate reptiles as a whole
Osteodermal cavity tissue serves the production of red blood cells (haematopoiesis)	Haematopoietic cells were found in the osteodermal cavities of reptiles and armadillos	Test significance of their contribution and investigate systematically
Air-filled osteodermal canals facilitate dermal respiration	Proposed for scincid lizards	It has been shown that the canals in question are not actually air-filled
Osteoderm are employed for inter- & intraspecific display	Proposed for thyreophoran dinosaurs	Test hypothesis in an extant model group, such as squamate reptiles
Osteoderms serve an ornamental function	Proposed without reference to a specific taxonomic group	By their very nature, ornaments are decorative rather than useful
Osteoderms serve camouflage	Proposed for chameleons	Show that osteoderms contribute to camouflage and explore if this can be replicated other squamate reptiles
Osteoderms provide protection from predation	Proposed for a variety of extant and extinct taxa. Penetration force tests indicate that *O. cataphractus* osteoderms can withstand mongoose bites	Test for a correlation in an extant model system, such as squamate reptiles. Biomechanical modelling for a range of extinct and extant taxa and their typical predators
Osteoderms provide protection from conspecifics	Proposed for a variety of extant and extinct taxa. Supported by ontogeny in cordylids and the gecko *Tarentola*	Test for a correlation in a larger model system, such as squamate reptiles. Biomechanical modelling for a range of extinct and extant taxa
Osteoderms provide protection from combative prey	Proposed for the gecko *Tarentola* and sand boas	Test for a correlation in a model system, such as squamate reptiles. Biomechanical modelling for a range of taxa and their typical prey
Osteoderms provide protection from environment	Proposed for caimans and short-limbed lizards	Test for a correlation (qualitative or quantitative) between the ventral osteoderm cover and limb length in a model system, such as squamate reptiles
Osteoderms contribute to burrowing	Proposed for osteoderm-bearing head-first burrowers. Supported by FEA	Test for a correlation (qualitative or quantitative) in a model system, such as squamate reptiles. Simulate burrowing strain with and without osteoderms using validated FE models
Osteoderm impair burrowing	Proposed for non-osteoderm-bearing head-first burrowers	
Osteoderms contribute to buoyancy regulation	Proposed mostly for extinct marine reptiles, but also for the marine iguana	Test with computational buoyancy simulations

Table 1 Continued.

Functional hypothesis	What is known	Future perspectives
Osteoderms contribute to hydrodynamics	Confirmed for the osteodermal ridges on the carapace of leatherback sea turtles by means of flow measurements	Test in other organisms for which this may apply using 3D prints or computational models (CFD)
A pronounced osteoderm cover is incompatible with aerial locomotion	Osteoderms are absent in highly derived lineages with aerial locomotion	Test in aerodynamic simulations for extant and extinct flying taxa with and without added weight
Osteoderms are part of a self-carrying bracing system	Has been proposed for extant crocodylians and the extinct Chroniosuchidae and Dissorophidae	Test using biomechanical simulations
A heavy osteoderm cover results in slower movement	Has been demonstrated in cordylid lizards	Investigate systematically in a larger taxonomic framework, such as squamate reptiles as a whole, using an appropriate comparative framework (i.e. using phylogenetically informed analyses)
Osteoderms contribute to skull biomechanics	Has been demonstrated by FEA and *in vivo* in scincid lizards	Investigate systematically in a larger taxonomic framework, such as squamate reptiles as a whole, both during transducer biting and feeding
Osteoderms serve radiative thermoregulation	Has been demonstrated with thermographic imaging in crocodylians, but more recent research could not replicate this	Resolve controversy. Investigate in a larger taxonomic framework, such as squamate reptiles, using both *in vitro* (passive properties) and *in vivo* testing (role of vascular network)
Osteoderms serve convective thermoregulation	Has been proposed for stegosaur back plates	There is no extant analogue for which to test this. Simulate convective heat exchange in a model
Osteoderms serve passive thermoregulation	Thermal insulation has been proposed for armadillos and shown for *Ouroborus* lizards in simulations, also supported by low *in vivo* cooling rates	Investigate systematically in a larger taxonomic framework, such as squamate reptiles as a whole, using *in vitro* measurements
Osteoderms serve as a calcium store	Proposed for cordylid lizards, titanosaurs and vertebrates in general. Supported by calcium shift from osteoderms to plasma in breeding female crocodiles	Investigate systematically in a larger taxonomic framework, such as squamate reptiles as a whole. Conduct experimental studies using *in vivo* μCT in females before, during and after being gravid
Osteoderms serve carbonate buffering and lactate sequestration	Inferred from observations in other hard tissues. In caimans, osteoderms were shown to account for up to 10% their buffering and sequestration capacity	Investigate systematically in a larger taxonomic framework, such as squamate reptiles as a whole
Osteoderms impact cutaneous gas exchange	Proposed for early tetrapods	Quantify cutaneous gas exchange in extant frogs with and without osteoderms
Osteoderms serve water retention in arid environments	The osteoderm-bearing skink *Ctenotus* has been shown to lose comparatively little water cutaneously. A correlation between osteoderm expression and aridity has been found in cordylid lizards	Investigate systematically in a larger taxonomic framework, such as squamate reptiles as a whole
Osteodermal cavity tissue serves the production of red blood cells (haematopoiesis)	Haematopoietic cells were found in the osteodermal cavities of reptiles and armadillos	Test significance of their contribution and investigate systematically
Air-filled osteodermal canals facilitate dermal respiration	Proposed for scincid lizards	It has been shown that the canals in question are not actually air-filled
Osteoderm are employed for inter- & intraspecific display	Proposed for thyreophoran dinosaurs	Test hypothesis in an extant model group, such as squamate reptiles
Osteoderms serve an ornamental function	Proposed without reference to a specific taxonomic group	By their very nature, ornaments are decorative rather than useful
Osteoderms serve camouflage	Proposed for chameleons	Show that osteoderms contribute to camouflage and explore if this can be replicated other squamate reptiles

anatomy (i.e. single versus compound, with or without capping layer, etc…) is directly related to overall body mobility. This data could be used to test for a trade-off between locomotion and protection. Finally, by instrumenting osteoderms with thermocouples and measuring heating and cooling rates both *in vivo* and *in vitro*, one could test hypotheses concerning the active or passive role of osteoderms in thermoregulation.

Squamate lizards offer a tremendous taxonomic and ecological diversity, but also a pronounced disparity in osteoderm form and presumed functions. Their repeated independent acquisition of osteoderms renders them an ideal model system to rigorously test evolutionary and functional hypotheses in a comparative phylogenetic framework. We propose that future comprehensive, systematic research into squamate osteoderm function may elucidate these aspects in extant taxa. Not only could this provide the basis for new biomimetic materials, but also shed light on the role that osteoderms may have played in the past and what impact they had on shaping present-day biodiversity.

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Author contributions

RE conceived the idea and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

References

Abel, O. (1901). *Über die Hautbepanzerung fossiler Zahnwale* (pp. 297–317). Beiträge zur Paläontologie von Österreich – Mitteilungen des Geol. und Paläontologischen Institutes der Univ Vol 13.

Abel, O. (1912). *Grundzüge der Palaeobiologie der Wirbeltiere*. E. Schweizerbart'sche Verlagsbuchhandlung.

Abel, O. (1919). *Die Stämme der Wirbeltiere*. W. de Gruyter.

Albertson, R. C., Cresko, W., Detrich, H. W., & Postlethwait, J. H. (2009). Evolutionary mutant models for human disease. *Trends in Genetics*, **25**, 74–81.

Alexander, D. E. (2015). *On the wing: Insects, pterosaurs, birds, bats and the evolution of animal flight*. Oxford University Press.

Alexander, R. M., Farina, R. A., & Vizcan, S. F. (1999). Tail blow energy and carapace fractures in a large glyptodont (Mammalia, Xenarthra). *Zoological Journal of the Linnean Society*, **126**, 41–49.

Anderson, C. V., Summers, A., & Zoological Research Museum Alexander Koenig. (2018). *Brookesia perarmata (zfmk:62848| ark:/87602/m4/M39276)*. www.morphosource.org/media/000039276

Anonymous. (1855). *Zu Delphinopsis freyerii Müll*. Sitzungsberichte der Akad. der Wissenschaften Math. Klasse 15, 345.

Arbour, V. M. (2009). Estimating impact forces of tail club strikes by ankylosaurid dinosaurs. *PLoS One*, **4**, e6738.

Arbour, V. M., & Zanno, L. E. (2020). Tail weaponry in ankylosaurs and glyptodonts: An example of a rare but strongly convergent phenotype. *The Anatomical Record*, **303**, 988–998.

Arbour, V. M., Zanno, L. E., & Evans, D. C. (2022). Palaeopathological evidence for intraspecific combat in ankylosaurid dinosaurs. *Biology Letters*, **18**, 20220404.

Arnold, E. N. (1973). Relationships of the palaearctic lizards assigned to the genera *Lacerta*, *Algyroides* and *Psammodromus* (Reptilia: Lacertidae). *Bulletin of the British Museum (Natural History). Zoology*, **25**, 291–366.

Arnold, E. N. (1998). Cranial kinesis in lizards: Variations, uses, and origins. In M. K. Hecht, R. J. MacIntyre, & M. T. Clegg (Eds.), *Evolutionary biology*, volume 30 (pp. 323–357). Plenum Press.

Arnold, E. N. (2002). *Holaspis*, a lizard that glided by accident: Mosaics of cooption and adaptation in a tropical forest lacertid (Reptilia, Lacertidae). *Bulletin of the Natural History Museum: Zoology Series*, **68**, 155–163.

Arnold, E. N., Arribas, O., & Carranza, S. (2007). *Systematics of the palaearctic and oriental lizard tribe Lacertini. Zootaxa*. Magnolia Press.

Bang, K., Kim, J., Lee, S.-I., & Choi, H. (2016). Hydrodynamic role of longitudinal dorsal ridges in a leatherback turtle swimming. *Scientific Reports*, **6**, 34283.

Bauer, A. M., & Russell, A. P. (1989). Supraorbital ossifications in geckos (Reptilia: Gekkonidae). *Canadian Journal of Zoology*, **67**, 678–684.

Baur, G. (1888). Unusual dermal ossifications. *Science*, **11**, 144.

Behrmann, G. (1996). De knobbeltjes op de rug-, staart- en borstvinnen van de bruinvis, *Phocoena phocoena* (Linné, 1758). *Marswin*, **17**, 66–76.

Bellairs, A. d.'A. (1970). *The life of reptiles* – Volume 2. Universe Books.

Berkovitz, B., & Shellis, P. (2017). *The teeth of non-mammalian vertebrates*. Elsevier.

Berman, D. S., Reisz, R. R., & Eberth, D. A. (1985). *Ecolsonia cutlerensis, an early Permian dissorophid amphibian from the cutler formation of north-central New Mexico*. New Mex. Bur. Mines Miner. Resour. New Mexico Bureau of Geology and Mineral Resources.

Bhullar, B.-A. S., & Bell, C. J. (2008). Osteoderms of the California legless lizard *Anniella* (Squamata: Anguidae) and their relevance for considerations of miniaturization. *Copeia*, **2008**, 785–793.

Blanchard, É. (1861). Recherches anatomiques et physiologiques sur le système tégumentaire des Reptiles (Sauriens et Ophidiens). *Annales des Sciences Naturelles: Zoologie*, **4**, 375–381.

Bonine, K. E., & Garland, T. J. (1999). Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. *Journal of Zoology*, **248**, 255–265.

Boulenger, G. A. (1887). *Catalogue of the lizards in the British Museum (Natural History)* – vol. III. Order of the Trustees.

Bour, R. (2008). Global diversity of turtles (Chelonii; Reptilia) in freshwater. *Hydrobiologia*, **595**, 593–598.

Broeckhoven, C., de Kock, C., & Mouton, P. L. F. N. (2017). Sexual dimorphism in osteoderm expression and the role of male intrasexual aggression. *Biological Journal of the Linnean Society*, **122**, 329–339.

Broeckhoven, C., Diedericks, G., & Mouton, P. l. F. N. (2015). What doesn't kill you might make you stronger: Functional basis for variation in body armour. *The Journal of Animal Ecology*, **84**, 1213–1221.

Broeckhoven, C., & du Plessis, A. (2022). Osteoderms as calcium reservoirs: Insights from the lizard *Ouroborus cataphractus*. *Journal of Anatomy*, **241**, 635–640.

Broeckhoven, C., du Plessis, A., & Hui, C. (2017). Functional trade-off between strength and thermal capacity of dermal armor: Insights from girdled lizards. *Journal of the Mechanical Behavior of Biomedical Materials*, **74**, 189–194.

Broeckhoven, C., du Plessis, A., Roux, S. G., Mouton, P. l. F. N., & Hui, C. (2017). Beauty is more than skin deep: A non-invasive protocol for in vivo anatomical study using micro-CT. *Methods in Ecology and Evolution*, **8**, 358–369.

Broeckhoven, C., El Adak, Y., Hui, C., Van Damme, R., & Stankowich, T. (2018). On dangerous ground: The evolution of body armour in cordyline lizards. *Proceedings of the Royal Society B: Biological Sciences*, **285**, 20180513.

Broeckhoven, C., Mouton, P. L. F. N., & Hui, C. (2018). Proximate causes of variation in dermal armour: Insights from armadillo lizards. *Oikos*, **127**, 1449–1458.

Buchwitz, M., Witzmann, F., Voigt, S., & Golubev, V. (2012). Osteoderm microstructure indicates the presence of a crocodylian-like trunk bracing system in a group of armoured basal tetrapods. *Acta Zoologica*, **93**, 260–280.

Burmeister, H. (1869). *Descripción de cuatro especies de Delfinides de la costa Argentina en el océano Atlántico*. An. del Mus. Público Buenos Aires 1.

Camacho, A., Navas, C. A., Yamanouchi, A. T., & Rodrigues, M. T. (2022). Consequences of evolving limbless, burrowing forms for the behavior and population density of tropical lizards. *Diversity*, **14**, 482.

Camp, C. L. (1923). Classification of the lizards. *Bulletin of the American Museum of Natural History*, **48**, 289–481.

Campbell, H. W. (1974). *Anelytropsis papillosus* cope – Mexican blind lizard. *Catalogue of American Amphibians and Reptiles*, **156**, 1–2.

Canei, J., & Nonclercq, D. (2021). Morphological study of the integument and corporal skeletal muscles of two psammophilous members of Scincidae (*Scincus scincus* and *Eumeces schneideri*). *Journal of Morphology*, **282**, 230–246.

Carpenter, K. (1998). Armor of *stegosaurus stenops*, and the taphonomic history of a new specimen from Garden Park, Colorado. *Modern Geology*, **23**, 127–144.

Carpenter, K., Sanders, F., McWhinney, L. A., & Wood, L. (2005). Evidence for predator-prey relationships: Examples for *Allosaurus* and *stegosaurus*. In K. Carpenter (Ed.), *The carnivorous dinosaurs* (pp. 325–350). Indiana University Press.

Carroll, R. L., & Zhi-Ming, D. (1991). *Hupehsuchus*, an enigmatic aquatic reptile from the Triassic of China, and the problem of establishing relationships. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **331**, 131–153.

Case, E. C. (1915). *The Permo-carboniferous red beds of North America and their vertebrate fauna*. Carnegie Institution of Washington.

Cebra-Thomas, J. A., Terrell, A., Branyan, K., Shah, S., Rice, R., Gyi, L., Yin, M., Hu, Y., Mangat, G., Simonet, J., Betters, E., & Gilbert, S. F. (2013). Late-emigrating trunk neural crest cells in turtle embryos generate an osteogenic ectomesenchyme in the plastron. *Developmental Dynamics*, **242**, 1223–1235.

Cerda, I. A., Desojo, J. B., Trotteyn, M. J., & Scheyer, T. M. (2015). Osteoderm histology of Proterochampsia and Doswelliidae (Reptilia: Archosauriformes) and their evolutionary and paleobiological implications. *Journal of Morphology*, **276**, 385–402.

Chapple, D. G. (2003). Ecology, life-history, and behavior in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetological Monographs*, **17**, 145–180.

Chen, I. H., Yang, W., & Meyers, M. A. (2015). Leatherback sea turtle shell: A tough and flexible biological design. *Acta Biomaterialia*, **28**, 2–12.

Chen, X., Motani, R., Cheng, L., Jiang, D., & Rieppel, O. (2015). A new specimen of Carroll's mystery hupehsuchian from the lower Triassic of China. *PLoS One*, **10**, e0126024.

Clack, J. A. (2012). *Gaining ground – The origin and evolution of tetrapods*. Indiana University Press.

Clarac, F., Campos, Z., & Marquis, O. (2024). The extended osteoderm shield in *Paleosuchus* sp.: A dwarf crocodylian adaptation to the equatorial forest ecosystem? *Comptes Rendus Palevol*, **23**.,161–170.

Clarac, F., Goussard, F., de Buffrénil, V., & Sansalone, V. (2019). The function(s) of bone ornamentation in the crocodylomorph osteoderms: A biomechanical model based on a finite element analysis. *Paleobiology*, **45**, 182–200.

Clarac, F., Goussard, F., Teresi, L., de Buffrénil, V., & Sansalone, V. (2017). Do the ornamented osteoderms influence

the heat conduction through the skin? A finite element analysis in Crocodylomorpha. *Journal of Thermal Biology*, **69**, 39–53.
Clarac, F., & Quilhac, A. (2019). The crocodylian skull and osteoderms: A functional exaptation to ectothermy? *Zoology*, **132**, 31–40.
Clarac, F., Scheyer, T. M., Desojo, J. B., Cerda, I. A., & Sanchez, S. (2020). The evolution of dermal shield vascularization in Testudinata and Pseudosuchia: Phylogenetic constraints versus ecophysiological adaptations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **375**, 20190132.
Clark, K., Bender, G., Murray, B. P., Panfilio, K., Cook, S., Davis, R., Murnen, K., Tuan, R. S., & Gilbert, S. F. (2001). Evidence for the neural crest origin of turtle plastron bones. *Genesis*, **31**, 111–117.
Coe, W. R., & Kunkel, B. W. (1906). Studies on the California limbless lizard, Anniella. *Transactions of the Kansas Academy of Science*, **12**, 349–403.
Coldiron, R. W. (1974). Possible functions of ornament in labyrinthodont amphibians. *Occasional papers of the Museum of Natural History (Lawrence)*, **33**, 1–19.
Conrad, J. L., Head, J. J., & Carrano, M. T. (2014). Unusual soft-tissue preservation of a crocodile lizard (Squamata, Shinisauria) from the Green River formation (Eocene) and shinisaur relationships. *The Anatomical Record*, **297**, 545–559.
Coombs, W. P. J. (1972). The bony eyelid of *Euoplocephalus* (Reptilia, Ornithischia). *Journal of Paleontology*, 637–650.**46**
Cooper, W., Van Wyk, J. H., Mouton, P. l. F. N., Al-Johany, A. M., Lemos-Espinal, J. A., Paulissen, M. A., & Flowers, M. (2000). Lizard antipredatory behaviors preventing extraction from crevices. *Herpetologica*, **56**, 394–401.
Dacke, C. G., Elsey, R. M., Trosclair, P. L., Sugiyama, T., Nevarez, J. G., & Schweitzer, M. H. (2015). Alligator osteoderms as a source of labile calcium for eggshell formation. *Journal of Zoology*, **297**, 255–264.
Dawson, W. R., Shoemaker, V. H., & Licht, P. (1966). Evaporative water losses of some small Australian lizards. *Ecology*, **47**, 589–594.
de Araújo Sena, M. V., & Cubo, J. (2023). Inferring the lifestyles of extinct Crocodyliformes using osteoderm ornamentation. *Science of Nature*, **110**, 41.
de Buffrénil, V. (1982). Morphogenesis of bone ornamentation in extant and extinct crocodilians. *Zoomorphology*, **99**, 155–166.
de Buffrénil, V., Canoville, A., D'Anastasio, R., & Domning, D. P. (2010). Evolution of sirenian pachyosteosclerosis, a model-case for the study of bone structure in aquatic tetrapods. *Journal of Mammalian Evolution*, **17**, 101–120.
de Buffrénil, V., Clarac, F., Canoville, A., & Laurin, M. (2016). Comparative data on the differentiation and growth of bone ornamentation in gnathostomes (Chordata: Vertebrata). *Journal of Morphology*, **277**, 634–670.
de Buffrénil, V., Dauphin, Y., Rage, J. C., & Sire, J. Y. (2011). An enamel-like tissue, osteodermine, on the osteoderms of a fossil anguid (Glyptosaurinae) lizard. *Comptes Rendus Palevol*, **10**, 427–437.
de Buffrénil, V., Farlow, J. O., & de Ricqlès, A. (1986). Growth and function of *stegosaurus* plates: Evidence from bone histology. *Paleobiology*, **12**, 459–473.
de Buffrénil, V., & Houssaye, A. (2021). Lepidosauria. In V. de Buffrénil, A. J. de Ricqlès, L. Zylberberg, & K. Padian (Eds.), *Vertebrate skeletal histology and paleohistology* (pp. 399–424). CRC Press, Taylor & Francis.
de Buffrénil, V., Sire, J.-Y., & Rage, J.-C. (2010). The histological structure of glyptosaurine osteoderms (Squamata: Anguidae), and the problem of osteoderm development in squamates. *Journal of Morphology*, **271**, 729–737.
de Buffrénil, V., & Zylberberg, L. (2021). Remarks on metaplastic processes in the skeleton. In V. de Buffrénil, A. J. de Ricqlès, L. Zylberberg, & K. Padian (Eds.), *Vertebrate skeletal histology and paleohistology* (pp. 247–256). CRC Press, Taylor & Francis.
de Queiroz, K. (1987). *Phylogenetic systematics of iguanine lizards: A comparative osteological study*. University of California Press.
de Ricqlès, A., de Buffrénil, V., & Laurin, M. (2021). Archosauromorpha: From early diapsids to archosaurs. In V. de Buffrénil, A. J. de Ricqlès, L. Zylberberg, & K. Padian (Eds.), *Vertebrate skeletal histology and paleohistology* (pp. 467–485). CRC Press, Taylor & Francis.
Delfino, M., Scheyer, T. M., Chesi, F., Fletcher, T., Gemel, R., Macdonald, S., Rabi, M., & Salisbury, S. W. (2013). Gross morphology and microstructure of type locality ossicles of *Psephophorus polygonus* Meyer, 1847 (Testudines, Dermochelyidae). *Geological Magazine*, **150**, 767–782.
DeMar, R. (1966). The phylogenetic and functional implications of the armor of the Dissorophidae. *Fieldiana: Geology (Chicago)*, **16**, 55–88.
DeMar, R. (1968). The Permian labyrinthodont amphibian *Dissorophus multicinctus*, and adaptations and phylogeny of the family Dissorophidae. *Journal of Paleontology*, **42**, 1210–1242.
Denison, R. H. (1968). Ordovician vertebrates from western United States. *Fieldiana: Geology (Chicago)*, **16**, 131–192.
Deraniyagala, P. E. P., Cantab, M. A., & Harvard, A. M. (1930). Testudinafce evolution. *Proceedings of the Zoological Society of London*, **100**, 1057–1070.
Dilkes, D. W. (2009). Comparison and biomechanical interpretations of the vertebrae and osteoderms of *Cacops aspidephorus* and *Dissorophus multicinctus* (Temnospondyli, Dissorophidae). *Journal of Vertebrate Paleontology*, **29**, 1013–1021.
Dilkes, D. W., & Brown, L. E. (2007). Biomechanics of the vertebrae and associated osteoderms of the early Permian amphibian *Cacops aspidephorus*. *Journal of Zoology*, **271**, 396–407.
Drane, C. R., & Webb, G. J. W. (1980). Functional morphology of the dermal vascular system of the Australian lizard *Tiliqua scincoides*. *Herpetologica*, **36**, 60–66.

Dubansky, B. H., & Dubansky, B. D. (2018). Natural development of dermal ectopic bone in the American alligator (*Alligator mississippiensis*) resembles heterotopic ossification disorders in humans. *The Anatomical Record*, **301**, 56–76.

Ebel, R., Müller, J., Ramm, T., Hipsley, C., & Amson, E. (2020a). *Dataset: μCT scans of the lepidosaur skull roof*. Museum für Naturkd. Berlin – Leibniz Inst. Evol. Biodiversity Science - Data Repos https://doi.org/10.7479/4k4c-yc83

Ebel, R., Müller, J., Ramm, T., Hipsley, C., & Amson, E. (2020b). First evidence of convergent lifestyle signal in reptile skull roof microanatomy. *BMC Biology*, **18**, 185.

English, L. T. (2018a). *Evolution of functional morphology of osteoderms across Crocodylomorpha*. The University of Texas at Austin.

English, L. T. (2018b). Variation in crocodilian dorsal scute organization and geometry with a discussion of possible functional implications. *Journal of Morphology*, **279**, 154–162.

Erickson, G. M., de Ricqlès, A., de Buffrénil, V., Molnar, R. E., & Bayless, M. K. (2003). Vermiform bones and the evolution of gigantism in *Megalania* — How a reptilian fox became a lion. *Journal of Vertebrate Paleontology*, **23**, 966–970.

Estes, R., de Queiroz, K., & Gauthier, J. A. (1988). Phylogenetic relationships within Squamata. In R. Estes & G. K. Pregill (Eds.), *Phylogenetic relationships of the lizard families: Essays commemorating Charles L.Camp* (pp. 119–281). Stanford University Press.

Evans, S. E., Groenke, J. R., Jones, M. E. H., Turner, A. H., & Krause, D. W. (2014). New material of *Beelzebufo*, a hyperossified frog (Amphibia: Anura) from the late cretaceous of Madagascar. *PLoS One*, **9**, e87236.

Farley, C., & Emshwiller, M. (1996). Efficiency of uphill locomotion in nocturnal and diurnal lizards. *The Journal of Experimental Biology*, **199**, 587–592.

Farlow, J. O., Hayashi, S., & Tattersall, G. J. (2010). Internal vascularity of the dermal plates of *Stegosaurus* (Ornithischia, Thyreophora). *Swiss Journal of Geosciences*, **103**, 173–185.

Farlow, J. O., Thompson, C. V., & Rosner, D. E. (1976). Plates of the dinosaur *Stegosaurus*: Forced convection heat loss fins? *Science*, **192**, 1123–1125.

Feder, M. E., & Burggren, W. W. (1985). Cutaneous gas exchange in vertebrates: Design, patterns, control and implications. *Biological Reviews of the Cambridge Philosophical Society*, **60**, 1–45.

Fogel, G. (2000). Observations on the giant sungazer lizard, *Cordylus giganteus*, in captivity. *Bulletin of the Chicago Herpetological Society*, **35**, 277–280.

Fogel, G. (2003). The art of armadillo lizards (*Cordylus cataphractus*): Fifteen years of captive observations. *Bulletin of the Chicago Herpetological Society*, **38**, 113–119.

Foster, K. L., Collins, C. E., Higham, T. E., & Garland, T. (2015). Determinants of lizard escape performance: Decision, motivation, ability, and opportunity. In W. E. Cooper, Jr. & D. T. Blumstein (Eds.), *Escaping from predators* (pp. 287–321). Cambridge University Press.

Francillon-Vieillot, H., de Buffrénil, V., Castanet, J., Géraudie, J., Meunier, F. J., Sire, J. Y., Zylberberg, L., & de Ricqlès, A. (1989). Microstructure and mineralization of vertebrate skeletal tissues. In J. G. Carter (Ed.), *Skeletal biomineralization: Patterns, processes and evolutionary trends*, volume 5 (pp. 471–530). American Geophysical Union.

Frey, E. (1988a). Anatomie des Körperstammes von *Alligator mississippiensis* Daudin. *Stuttgarter Beiträge Naturkunde Serie A*, **424**, 106.

Frey, E. (1988b). Das Tragesystem der Krokodile – Eine biomechanische und phylogenetische Analyse. *Stuttgarter Beiträge Naturkunde Serie A*, **426**.,1–60.

Fry, B. G. (Ed.). (2015). *Venomous reptiles and their toxins*. Oxford University Press.

Frýdlová, P., Janovská, V., Mrzílková, J., Halašková, M., Riegerová, M., Dudák, J., Tymlová, V., Žemlička, J., Zach, P., & Frynta, D. (2023). The first description of dermal armour in snakes. *Scientific Reports*, **13**, 6405.

Gadow, H. (1901). *Amphibia and reptiles*. Macmillan and Co., limited.

Gauthier, J. A., Kearney, M., Maisano, J. A., Rieppel, O., & Behlke, A. D. B. (2012). Assembling the squamate tree of life: Perspectives from the phenotype and the fossil record. *Bulletin of the Peabody Museum of Natural History*, **53**, 3–308.

Gilbert, S. F., Bender, G., Betters, E., Yin, M., & Cebra-Thomas, J. A. (2007). The contribution of neural crest cells to the nuchal bone and plastron of the turtle shell. *Integrative and Comparative Biology*, **47**, 401–408.

Ginter, C. C., Böttger, S. A., & Fish, F. E. (2011). Morphology and microanatomy of harbor porpoise (*Phocoena phocoena*) dorsal fin tubercles. *Journal of Morphology*, **272**, 27–33.

Glaeser, G., Paulus, H. F., & Nachtigall, W. (2017). *The evolution of flight*. Springer International Publishing.

Goldberg, S., Venkatesh, A., Martinez, J., Dombroski, C., Abesamis, J., Campbell, C., Mccalipp, M., & de Bellard, M. E. (2020). The development of the trunk neural crest in the turtle *Trachemys scripta*. *Developmental Dynamics*, **249**, 125–140.

Gray, J., & Florida Museum of Natural History. (2023). *Chalcides ocellatus (uf:Herp:133931 | ark:/87602/m4/574627)*. www.morphosource.org/media/000574627

Greer, A. E. (2007). *The biology and evolution of scincid lizards*. Sydney: online @academia.edu.

Griffing, A. H., Daza, J. D., Deboer, J. C., & Bauer, A. M. (2018). Developmental osteology of the parafrontal bones of the Sphaerodactylidae. *The Anatomical Record*, **301**, 581–606.

Haines, R. W., & Mohuiddin, A. (1968). Metaplastic bone. *Journal of Anatomy*, **103**, 527–538.

Hammel, H. T., Caldwell, F. T., & Abrams, R. M. (1967). Regulation of body temperature in the blue-tongued lizard. *Science*, **156**, 1260–1262.

Hayashi, S., Carpenter, K., Scheyer, T. M., Watabe, M., & Suzuki, D. (2010). Function and evolution of ankylosaur dermal armor. *Acta Palaeontologica Polonica*, **55**, 213–228.

Hayashi, S., Carpenter, K., Watabe, M., & McWhinney, L. A. (2012). Ontogenetic histology of *Stegosaurus* plates and spikes. *Palaeontology*, **55**, 145–161.

Heacock, P., Cassidy, C.-J. V., Bollard, J. K., & Plier, J. (Eds.). (2009). *Cambridge academic content dictionary* (1st ed.). Cambridge University Press.

Hendrickx, C., & Bell, P. R. (2021). The scaly skin of the abelisaurid *Carnotaurus sastrei* (Theropoda: Ceratosauria) from the upper cretaceous of Patagonia. *Cretaceous Research*, **128**, 104994.

Hendrickx, C., Bell, P. R., Pittman, M., Milner, A. R. C., Cuesta, E., O'Connor, J., Loewen, M., Currie, P. J., Mateus, O., Kaye, T. G., & Delcourt, R. (2022). Morphology and distribution of scales, dermal ossifications, and other non-feather integumentary structures in non-avialan theropod dinosaurs. *Biological Reviews*, **97**, 960–1004.

Heyer, W. R. (1972). A new limbless skink (Reptilia: Scincidae) from Thailand with comments on the generic status of the limbless skinks of Southeast Asia. *Fieldiana Zoology*, **58**, 109–129.

Hill, R. V. (2006). Comparative anatomy and histology of xenarthran osteoderms. *Journal of Morphology*, **267**, 1441–1460.

Hirasawa, T., Nagashima, H., & Kuratani, S. (2013). The endoskeletal origin of the turtle carapace. *Nature Communications*, **4**, 2107.

Hoffstetter, P. R. (1962). Observations sur les ostéodermes et la classification des anguidés actuels et fossils (Reptiles, Sauriens). *Bulletin du Muséum National D'Histoire Naturelle*, **34**, 149–157.

Hölldobler, B., & Wilson, E. O. (1990). *The ants*. Belknap Press.

Hoofien, J. H. (1962). An unusual congregation of the gekkonid lizard *Tarentola annularis* (Geoffroy). *Herpetologica*, **18**, 54–56.

Hoyer, R. F. (1974). Description of a rubber boa (*Charina bottae*) population from western Oregon. *Herpetologica*, **30**, 275–283.

Hua, S., & de Buffrénil, V. (1996). Bone histology as a clue in the interpretation of functional adaptations in the Thalattosuchia (Reptilia, Crocodylia). *Journal of Vertebrate Paleontology*, **16**, 703–717.

Hutchinson, M. N., Milne, T., & Croft, T. (1994). Redescription and ecological notes on the pygmy bluetongue, *Tiliqua adelaidensis* (Squamata: Scincidae). *Transactions of the Royal Society of South Australia*, **118**, 217–226.

Inacio Veenstra, L. L., & Broeckhoven, C. (2022). Revisiting the thermoregulation hypothesis of osteoderms: A study of the crocodilian *Paleosuchus palpebrosus* (Crocodilia: Alligatoridae). *Biological Journal of the Linnean Society*, **135**, 679–691.

Jackson, D. C. (1997). Lactate accumulation in the shell of the turtle *Chrysemys picta bellii* during anoxia at 3°C and 10°C. *The Journal of Experimental Biology*, **200**, 2295–2300.

Jackson, D. C., Andrade, D. V., & Abe, A. S. (2003). Lactate sequestration by osteoderms of the broad-nose caiman, *Caiman latirostris*, following capture and forced submergence. *The Journal of Experimental Biology*, **206**, 3601–3606.

Jackson, D. C., & Heisler, N. (1982). Plasma ion balance of submerged anoxic turtles at 3°C: The role of calcium lactate formation. *Respiration Physiology*, **49**, 159–174.

Janis, C. M., Devlin, K., Warren, D. E., & Witzmann, F. (2012). Dermal bone in early tetrapods: A palaeophysiological hypothesis of adaptation for terrestrial acidosis. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 3035–3040.

Janis, C. M., Napoli, J. G., & Warren, D. E. (2020). Palaeophysiology of pH regulation in tetrapods. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **375**, 20190131.

Janvier, P. (1996). *Early vertebrates*. Clarendon Press.

Janvier, P. (2015). Facts and fancies about early fossil chordates and vertebrates. *Nature*, **520**, 483–489.

Jared, C., Antoniazzi, M. M., Navas, C. A., Katchburian, E., Freymüller, E., Tambourgi, D. V., & Rodrigues, M. T. (2005). Head co-ossification, phragmosis and defence in the casque-headed tree frog *Corythomantis greeningi*. *Journal of Zoology*, **265**, 1–8.

Jørgensen, S. E., & Fath, B. D. (Eds.). (2008). *Encyclopedia of ecology* (1st ed.). Elsevier B.V.

Jusufi, A., Le Verger, K., Lonneux, O., Ramstein, N., Sánchez-Villagra, M., Scheyer, T. M., & Ijspeert, A. (2023). *PaleoRobotic reconstruction of a mammalian knight: When evolution leads to armor and tail weaponry*. In *International Symposium on Palaeo-bioinspiration*. Paris.

Kawashima, T., Thorington, R. W., Bohaska, P. W., Chen, Y. J., & Sato, F. (2015). Anatomy of shoulder girdle muscle modifications and walking adaptation in the scaly chinese pangolin (*Manis pentadactyla pentadactyla: Pholidota*) compared with the partially osteoderm-clad armadillos (Dasypodidae). *The Anatomical Record*, **298**, 1217–1236.

Kerbert, C. (1877). Ueber die Haut der Reptilien und anderer Wirbelthiere. *Archiv für Mikroskopische Anatomie*, **13**, 205–262.

Kéver, L., Olivier, D., Marghoub, A., Evans, S. E., Vickaryous, M. K., Moazen, M., & Herrel, A. (2022). Biomechanical behaviour of lizard osteoderms and skin under external loading. *Journal of Experimental Biology*, **225**.,1–14.

Khalil, F., & Abdel-Messeih, G. (1962a). Tissue constituents of reptiles in relation to their mode of life – II: Lipid content. *Biochemistry & Physiology*, **6**, 171–174.

Khalil, F., & Abdel-Messeih, G. (1962b). Tissue constituents of reptiles in relation to their mode of life – I: Water content. *Biochemistry and Physiology*, **5**, 327–330.

Kirby, A. C. (2020). *A characterisation of the integumentary skeleton of lizards (Reptilia: Squamata)*. University College London.

Kirby, A. C., Vickaryous, M. K., Boyde, A., Olivo, A., Moazen, M., Bertazzo, S., & Evans, S. (2020). A comparative histological study of the osteoderms in the lizards *Heloderma suspectum* (Squamata: Helodermatidae) and *Varanus komodoensis* (Squamata: Varanidae). *Journal of Anatomy*, **236**, 1035–1043.

Klein, N., Scheyer, T. M., & Tütken, T. (2009). Skeletochronology and isotopic analysis of a captive individual of *Alligator mississippiensis* Daudin, 1802. *Fossil Record*, **12**, 121–131.

Kofron, C. P. (1990). The reproductive cycle of the Nile crocodile (*Crocodylus niloticus*). *Journal of Zoology*, **221**, 477–488.

Kohlsdorf, T., Garland, T., & Navas, C. A. (2001). Limb and tail lengths in relation to substrate usage in *Tropidurus* lizards. *Journal of Morphology*, **248**, 151–164.

Krmpotic, C. M., Ciancio, M. R., Carlini, A. A., Castro, M. C., Scarano, A. C., & Barbeito, C. G. (2015). Comparative histology and ontogenetic change in the carapace of armadillos (Mammalia: Dasypodidae). *Zoomorphology*, **134**, 601–616.

Krmpotic, C. M., Nishida, F., Galliari, F. C., Pombo, M. T., Acuña, F., Barbeito, C. G., & Carlini, A. A. (2021). The dorsal integument of the southern long-nosed armadillo *Dasypus hybridus* (Cingulata, Xenarthra), and a possible neural crest origin of the osteoderms. Discussing evolutive consequences for Amniota. *Journal of Mammalian Evolution*, **28**, 635–645.

Krmpotic, C. M., Scarano, A. C., Andrés Laube, P. F., Ciancio, M. R., Loza, C. M., Acuña, F., Castro, N. N., & Barbeito, C. G. (2024). The double skin of the pink fairy armadillo, the peculiar integumentary system of *Chlamyphorus truncatus* Cingulata (Mammalia, Xenarthra). *Journal of Zoology*, **322**, 203–220.

Kükenthal, W. (1889). *Vergleichend-anatomische und entwicklungsgeschichtliche Untersuchungen an Walthieren*. Verlag von Gustav Fischer.

Laurin, M., Canoville, A., & Germain, D. (2011). Bone microanatomy and lifestyle: A descriptive approach. *Comptes Rendus Palevol*, **10**, 381–402.

Laver, R. J., Morales, C. H., Heinicke, M. P., Gamble, T., Longoria, K., Bauer, A. M., & Daza, J. D. (2020). The development of cephalic armor in the tokay gecko (Squamata: Gekkonidae: *Gekko gecko*). *Journal of Morphology*, **281**, 213–228.

Leach, W. J. (1961). *Functional anatomy: Mammalian and comparative* (3rd ed.). McGraw-Hill Book Company, Inc.

Lee, M. S. Y. (1997). A taxonomic revision of pareiasaurian reptiles: Implications for Permain terrestrial palaeoecology. *Modern Geology*, **21**, 231–298.

Leenders, T. (2019). *Reptiles of Costa Rica – A field guide*. Cornell University Press.

Legendre, L. J., Guénard, G., Botha-Brink, J., & Cubo, J. (2016). Palaeohistological evidence for ancestral high metabolic rate in archosaurs. *Systematic Biology*, **65**, 989–996.

Levrat-Calviac, V. (1986). Étude comparée des ostéodermes de *Tarentola mauritanica* et de *T. neglecta* (Gekkonidae, Squamata). *Archives d'Anatomie Microscopique et de Morphologie Expérimentale*, **75**, 29–43.

Levrat-Calviac, V., & Zylberberg, L. (1986). The structure of the osteoderms in the gekko: *Tarentola mauritanica*. *The American Journal of Anatomy*, **176**, 437–446.

Leydig, F. (1857). *Lehrbuch der Histologie des Menschen und der Thiere*. Verlag von Meidinger Sohn & Comp.

Leydig, F. (1868). *Ueber Organe eines sechsten Sinnes – Zugleich als Beitrag zur Kenntniss des feineren Baues der Haut der Amphibien und Reptilien*. E. Blochmann & Sohn.

Li, C., Jiang, D. Y., Cheng, L., Wu, X. C., & Rieppel, O. (2014). A new species of *Largocephalosaurus* (Diapsida: Saurosphargidae), with implications for the morphological diversity and phylogeny of the group. *Geological Magazine*, **151**, 100–120.

Li, C., Rieppel, O., Wu, X.-C., Zhao, L.-J., & Wang, L.-T. (2011). A new Triassic marine reptile from southwestern China. *Journal of Vertebrate Paleontology*, **31**, 303–312.

Li, C., Wu, X., Zhao, L., Nesbitt, S. J., Stocker, M. R., & Wang, L.-T. (2016). A new armored archosauriform (Diapsida: Archosauromorpha) from the marine middle Triassic of China, with implications for the diverse life styles of archosauriforms prior to the diversification of Archosauria. *Science of Nature*, **103**, 95.

Losos, J. B., Mouton, P. L. F. N., Bickel, R., Cornelius, I., & Ruddock, L. (2002). The effect of body armature on escape behaviour in cordylid lizards. *Animal Behaviour*, **64**, 313–321.

Lyson, T. R., Bever, G. S., Scheyer, T. M., Hsiang, A. Y., & Gauthier, J. A. (2013). Evolutionary origin of the turtle shell. *Current Biology*, **23**, 1113–1119.

Lyson, T. R., Rubidge, B. S., Scheyer, T. M., de Queiroz, K., Schachner, E. R., Smith, R. M. H., Botha-Brink, J., & Bever, G. S. (2016). Fossorial origin of the turtle shell. *Current Biology*, **26**, 1887–1894.

Maden, M., Polvadore, T., Polanco, A., Barbazuk, W. B., & Stanley, E. (2023). Osteoderms in a mammal the spiny mouse Acomys and the independent evolution of dermal armor. *iScience*, **26**, 106779.

Magalhães, R. A., Feijó, A., Bocchiglieri, A., de Sena, L. M. M., Attias, N., & Rodrigues, F. H. G. (2022). Cephalic shield morphology as species diagnostic trait and individual natural mark in three-banded armadillos (Tolypeutes; Cingulata: Chlamyphoridae). *Mammalia*, **86**, 632–640.

Main, R. P., de Ricqlès, A., Horner, J. R., & Padian, K. (2005). The evolution and function of thyreophoran dinosaur scutes: Implications for plate function in stegosaurs. *Paleobiology*, **31**, 291–314.

Maisano, J. A., Laduc, T. J., Bell, C. J., & Barber, D. (2019). The cephalic osteoderms of *Varanus komodoensis* as revealed by high-resolution x-ray computed tomography. *The Anatomical Record*, **302**, 1675–1680.

Maliuk, A., Marghoub, A., Williams, C. J. A., Stanley, E., Kéver, L., Vickaryous, M., Herrel, A., Evans, S. E., & Moazen, M. (2024). Comparative analysis of osteoderms across the lizard body. *The Anatomical Record*, **307**, 1–13.

Marghoub, A., Kéver, L., Williams, C. J. A., Abzhanov, A., Vickaryous, M. K., Herrel, A., Evans, S. E., & Moazen, M. (2023). The role of cranial osteoderms on the mechanics of the skull in scincid lizards. *The Anatomical Record*, **306**, 1–10.

Marghoub, A., Williams, C. J. A., Leite, J. V., Kirby, A. C., Kéver, L., Porro, L. B., Barrett, P. M., Bertazzo, S., Abzhanov, A., Vickaryous, M. K., Herrel, A., Evans, S. E., & Moazen, M. (2022). Unravelling the structural variation of lizard osteoderms. *Acta Biomaterialia*, **146**, 306–316.

Marinho, T. D. S. (2007). Functional aspects of titanosaur osteoderms. *Nature Precedings*, **30**, 251.

Marinho, T. D. S., & Iori, F. V. (2011). A large titanosaur (Dinosauria, Sauropoda) osteoderm with possible bite marks from Ibirá, São Paulo state, Brazil. In *Paleontologia: Cenários de Vida*, Vol. 4 (pp. 339–349). Interciência; Cincias Biol—Gicas e Naturais edition.

Marshall, A. J. (Ed.). (1960). *Biology and comparative physiology of birds: volume I*. Academic Press.

Martin, S. (2008). Global diversity of crocodiles (Crocodilia, Reptilia) in freshwater. *Hydrobiologia*, **595**, 587–591.

Martinez, J., & Harvard Museum of Comparative Zoology. (2019). *Ceratophrys cranwelli (mcz:Herp:A35360 | ark:/87602/m4/M70811)*. www.morphosource.org/media/000070811

Mautner, A.-K., Latimer, A. E., Fritz, U., & Scheyer, T. M. (2017). An updated description of the osteology of the pancake tortoise *Malacochersus tornieri* (Testudines: Testudinidae) with special focus on intraspecific variation. *Journal of Morphology*, **278**, 321–333.

McDowell, S. B. J., & Bogert, C. M. (1954). The systematic position of *Lanthanotus* and the affinities of the anguimorphan lizards. *Bulletin of the American Museum of Natural History*, **105**, 1–142.

Melville, J., & Swain, R. (2000). Evolutionary relationships between morphology, performance and habitat openness in the lizard genus *Niveoscincus* (Scincidae: Lygosominae). *Biological Journal of the Linnean Society*, **70**, 667–683.

Milne, T., & Bull, C. M. (2000). Burrow choice by individuals of different sizes in the endangered pygmy blue tongue lizard *Tiliqua adelaidensis*. *Biological Conservation*, **95**, 295–301.

Miralles, A., Hipsley, C. A., Erens, J., Gehara, M., Rakotoarison, A., Glaw, F., Müller, J., & Vences, M. (2015). Distinct patterns of desynchronized limb regression in Malagasy scincine lizards (Squamata, Scincidae). *PLoS One*, **10**, e0126074.

Mondéjar-Fernández, J., Clément, G., & Sanchez, S. (2014). New insights into the scales of the Devonian tetrapod *Tulerpeton curtum* Lebedev, 1984. *Journal of Vertebrate Paleontology*, **34**, 1454–1459.

Mondéjar-Fernández, J., & Janvier, P. (2021). Finned vertebrates. In V. de Buffrénil, A. J. de Ricqlès, L. Zylberberg, & K. Padian (Eds.), *Vertebrate skeletal histology and paleohistology* (pp. 294–324). CRC Press, Taylor & Francis.

Mongera, A., & Nüsslein-Volhard, C. (2013). Scales of fish arise from mesoderm. *Current Biology*, **23**, R338–R339.

Moss, M. L. (1969). Comparative histology of dermal sclerifications in reptiles. *Acta Anatomica (Basel)*, **73**, 510–533.

Moss, M. L. (1972). The vertebrate dermis and the integumental skeleton. *American Zoologist*, **12**, 27–34.

Müller, J. P. (1853). Bericht über ein neu entdecktes Cetaceum aus Radoboy, *Delphinopsis freyerii*. *Sitzungsberichte der Akad. der Wissenschaften Math. Klasse*, **10**, 84–88.

Murphy, J. B., Mendyk, R. W., Miller, K. L., & Augustine, L. (2019). Tales of monitor lizard tails and other perspectives. *Herpetological Review*, **50**, 178–201.

Niethammer, J. (1975). Hautverknöcherungen im Schwanz von Stachelmäusen (*Acomys dimidiatus*). *Bonn Zoological Bulletin*, **26**, 100–106.

Otto, H. (1909). *Die Beschuppung der Brevilinguier und Ascalaboten*. Jenaische Zeitschrift für Naturwiss.

Paluh, D. J., Griffing, A. H., & Bauer, A. M. (2017). Sheddable armour: Identification of osteoderms in the integument of *Geckolepis maculata* (Gekkota). *African Journal of Herpetology*, **66**, 12–24.

Paluh, D. J., Stanley, E. L., & Blackburn, D. C. (2020). Evolution of hyperossification expands skull diversity in frogs. *Proceedings of the National Academy of Sciences of the United States of America*, **117**, 1–9.

Pandelis, G., & Long, C. (2018). *Adolfus africanus (cas: Herp:201658|ark:/87602/m4/M63817)*. www.morphosource.org/media/000063817

Patchell, F. C., & Shine, R. (1986). Hinged teeth for hard-bodied prey: A case of convergent evolution between snakes and legless lizards. *Journal of Zoology*, **208**, 269–275.

Petrozzi, F., Hema, E. M., Demaya, G. S., Benansio, J. S., Eniang, E. A., Diagne, T., Segniagbeto, G. H., & Luiselli, L. (2020). *Centrochelys sulcata* (Miller 1779). In Anders G.J. Rhodin, John B. Iverson, Peter Paul van Dijk, Craig B. Stanford, Eric V. Goode, Kurt A. Buhlmann, Russell A.Mittermeier.*Conservation biology of freshwater turtles and tortoises: A compilation project of the IUCN/SSC tortoise and freshwater turtle specialist group* (pp. 110.1–110.16). IUCN/SSC Tortoises and Freshwater Turtles Spacialist Group.

Pianka, E. R., & Vitt, L. J. (2003). *Lizards: Windows to the evolution of diversity*. University of California Press.

Pochat-Cottilloux, Y., Martin, J. E., Amiot, R., Cubo, J., & de Buffrénil, V. (2023). A survey of osteoderm histology and ornamentation among Crocodylomorpha: A new proxy to infer lifestyle? *Journal of Morphology*, **284**, 1–11.

Prötzel, D., Heß, M., Scherz, M. D., Schwager, M., Padje, A. v.'t., & Glaw, F. (2018). Widespread bone-based fluorescence in chameleons. *Scientific Reports*, **8**, 698.

Pyron, R. A., Burbrink, F. T., & Wiens, J. J. (2013). A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*, **13**, 93.

Quinzio, S., & Fabrezi, M. (2012). Ontogenetic and structural variation of mineralizations and ossifications in the integument within ceratophryid frogs (Anura, Ceratophryidae). *The Anatomical Record*, **295**, 2089–2103.

Revan, A. (2011). *Reconstructing an icon: Historical significance of the Peabody's mounted skeleton of stegosaurus and the changes necessary to make it correct anatomically*. Yale University.

Rieppel, O. (1981). The skull and the jaw adductor musculature in some burrowing scincomorph lizards of the genera *Acontias*, *Typhlosaurus* and *Feylinia*. *Journal of Zoology*, **195**, 493–528.

Rieppel, O. (2000). Sauropterygia I – Placodontia, Pachypleurosauria, Nothosauroidea, Pistosauroidea. In Peter Wellnhofer. *Handbuch der Paläoherpetologie – Part 12A* (pp. 1–134). Dr. Friedrich Pfeil.

Rieppel, O. (2002). *The dermal armor of the cyamodontoid placodonts (Reptilia, Sauropterygia): Morphology and systematic value*. Fieldiana Geol Chicago. Field Museum of Natural History.

Robertson, P., & Coventry, A. J. (2019). *Reptiles of Victoria: A guide to identification and ecology*. CSIRO Publishing.

Rockhold, H., Krech, J., & Ohio University. (2019). *Chelydra serpentina (ouvc:10681 | ark:/87602/m4/M76034)*. www.morphosource.org/media/000076034

Rogers, K. A. C., & D'Emic, M. D. (2012). Triumph of the titans. *Scientific American*, **306**, 48–55.

Romer, A. S. (1947). Review of the Labyrinthodontia. *Bulletin of the Museum of Comparative Zoology at Harvard College*, **99**, 1–368.

Romer, A. S. (1956). *Osteology of the reptiles*. University of Chicago Press.

Ruibal, R., & Shoemaker, V. (1984). Osteoderms in anurans. *Journal of Herpetology*, **18**, 313–328.

Rutland, C. S., Cigler, P., & Kubale, V. (2019). Reptilian skin and its special histological structures. In Catrin Sian Rutland, Valentina Kubale. *Veterinary anatomy and physiology* (pp. 1–21). IntechOpen.

Saitta, E. T. (2015). Evidence for sexual dimorphism in the plated dinosaur *Stegosaurus mjosi* (Ornithischia, Stegosauria) from the Morrison formation (Upper Jurassic) of western USA. *PLoS One*, **10**, e0123503.

Salgado-Ahumada, J. S., Ercoli, M. D., Álvarez, A., Castro, M. C., & Ciancio, M. R. (2023). Geometric morphometrics as a tool to identify Dasypodini osteoderms: Implications for the oldest records of *Dasypus*. *Journal of Mammalian Evolution*, **30**, 597–614.

Salisbury, S. W., & Frey, E. (2000). A biomechanical transformation model for the evolution of semi-spheroidal articulations between adjoining vertebral bodies in crocodilians. In Gordon C. Grigg, Frank Seebacher, Craig E. Franklin.*Crocodilian biology and evolution*. Surrey Beatty & Sons Pty Limited.

Sanchez, S., Clarac, F., Laurin, M., & de Ricqlès, A. (2021). Early tetrapodomorphs. In V. de Buffrénil, A. J. de Ricqlès, L. Zylberberg, & K. Padian (Eds.), *Vertebrate skeletal histology and paleohistology* (pp. 325–344). CRC Press, Taylor & Francis.

Sansom, I. J., Donoghue, P. C. J., & Albanesi, G. (2005). Histology and affinity of the earliest armoured vertebrate. *Biology Letters*, **1**, 446–449.

Savitzky, A. H. (1981). Hinged teeth in snakes: An adaptation for swallowing hard-bodied prey. *Science*, **212**, 346–349.

Scarano, A. C., Ciancio, M. R., Barbeito-Andrés, J., Barbeito, C. G., & Krmpotic, C. M. (2020). Micromorphology of osteoderms in Dasypodidae (Cingulata, Mammalia): Characterization and 3D-reconstructions. *Journal of Morphology*, **281**, 258–272.

Scheyer, T. M. (2007). Skeletal histology of the dermal armor of Placodontia: The occurrence of 'postcranial fibro-cartilaginous bone' and its developmental implications. *Journal of Anatomy*, **211**, 737–753.

Scheyer, T. M., Brüllmann, B., & Sánchez-Villagra, M. R. (2008). The ontogeny of the shell in side-necked turtles, with emphasis on the homologies of costal and neural bones. *Journal of Morphology*, **269**, 1008–1021.

Scheyer, T. M., Martin Sander, P., Joyce, W. G., Böhme, W., & Witzel, U. (2007). A plywood structure in the shell of fossil and living soft-shelled turtles (Trionychidae) and its evolutionary implications. *Organisms, Diversity and Evolution*, **7**, 136–144.

Scheyer, T. M., Neenan, J. M., Bodogan, T., Furrer, H., Obrist, C., & Plamondon, M. (2017). A new, exceptionally preserved juvenile specimen of *Eusaurosphargis dalsassoi* (Diapsida) and implications for Mesozoic marine diapsid phylogeny. *Scientific Reports*, **7**, 4406.

Scheyer, T. M., Pérez-García, A., & Murelaga, X. (2015). Shell bone histology of solemydid turtles (stem Testudines): Palaeoecological implications. *Organisms, Diversity and Evolution*, **15**, 199–212.

Scheyer, T. M., & Sander, P. M. (2004). Histology of ankylosaur osteoderms: Implications for systematics and function. *Journal of Vertebrate Paleontology*, **24**, 874–893.

Scheyer, T. M., & Sander, P. M. (2009). Bone microstructures and mode of skeletogenesis in osteoderms of three pareiasaur taxa from the Permian of South Africa. *Journal of Evolutionary Biology*, **22**, 1153–1162.

Schmidt, K. P. (1955). Phragmosis: Animals with buit-in doors. *Chicago Museum of Natural History Bulletin*, **26**, 2.

Schmidt, W. J. (1911). *Beobachtungen an der Haut von Geckolepis und einigen anderen Geckoniden*. Reise Ostafrika den Jahren 1903-1905 mit Mitteln der Hermann und Elise geb. Heckmann Wentzel-Stiftung ausgeführt von Profr. Dr. Alfred Voeltzkow 4.

Schmidt, W. J. (1912). Studien am Integument der Reptilien – III. Über die Haut der Gerrhosauriden. *Zool. Jahrbücher Jena – Abteilung für Anat. und Ontog. der Tiere*, **35**, 75–104.

Schmidt, W. J. (1914). Studien am Integument der Reptilien – VI. Über die Knochenschuppen der Crocodile. *Zool. Jahrbücher Jena – Abteilung für Anat. und Ontog. der Tiere*, **38**, 643–666.

Schucht, P. J., Rühr, P. T., Geier, B., Glaw, F., & Lambertz, M. (2020). Armored with skin and bone: A combined histological and µCT-study of the exceptional integument of the Antsingy leaf chameleon *Brookesia perarmata* (Angel, 1933). *Journal of Morphology*, **281**, 754–764.

Seidel, M. R. (1979). The osteoderms of the American alligator and their functional significance. *Herpetologica*, **35**, 375–380.

Seymour, R. S., Bennett-Stamper, C. L., Johnston, S. D., Carrier, D. R., & Grigg, G. C. (2004). Evidence for endothermic ancestors of crocodiles at the stem of archosaur evolution. *Physiological and Biochemical Zoology*, **77**, 1051–1067.

Shine, R. (1991). *Australian snakes – A natural history*. Reed New Holland Publishers Pty Ltd.

Sibert, E., Gage, M., & Yale Peabody Museum. (2018). *Gerrhonotus infernalis (ypm:Vz:Herr 14547 | ark:/87602/m4/M57811)*. www.morphosource.org/media/000057811

Silva, J. C. G. J., Montefeltro, F. C., Marinho, T. S., Martinelli, A. G., & Langer, M. C. (2022). Finite elements analysis suggests a defensive role for osteoderms in titanosaur dinosaurs (Sauropoda). *Cretaceous Research*, **129**, 105031.

Sire, J.-Y., Donoghue, P. C. J., & Vickaryous, M. K. (2009). Origin and evolution of the integumentary skeleton in non-tetrapod vertebrates. *Journal of Anatomy*, **214**, 409–440.

Smith, M. A. (1935). *The fauna of British India, including Ceylon and Burma – Reptilia and Amphibia*, vol. II – sauria. Taylor and Francis.

Smith, M. M., & Hall, B. K. (1990). Development and evolutionary origins of vertebrate skeletogenic and odontogenic tissues. *Biological Reviews of the Cambridge Philosophical Society*, **65**, 277–373.

Sridhar, V., Prestridge, H., & Texas A&M University. (2018). *Alligator sinensis (tcwc:Herpetology:86174|ark:/87602/m4/M55818)*. www.morphosource.org/media/000055818

Stanley, E., & Florida Museum of Natural History. (2020). *Gekko gecko* (uf:herp:83669|ark:/87602/m4/M99373). www.morphosource.org/media/000099373

Stanley, E., & Florida Museum of Natural History. (2021). *Ouroborus cataphractus (uf:herp:191433|ark:/87602/m4/359089)*. www.morphosource.org/media/000359089

Stanley, E., & Florida Museum of Natural History. (2022a). *Eryx colubrinus (uf:herp:151340|ark:/87602/m4/476408)*. www.morphosource.org/media/000476408

Stanley, E., & Florida Museum of Natural History. (2022b). *Heloderma horridum (uf:herp:153328|ark:/87602/m4/446464)*. www.morphosource.org/media/000446464

Stanley, E., & Florida Museum of Natural History. (2022c). *Varanus timorensis (uf:herp:137865|ark:/87602/m4/456653)*. www.morphosource.org/media/000456653

Stanley, E., & Yale Peabody Museum. (2019). *Testudo graeca (ypm:vz:herr 2925|ark:/87602/m4/M72844)*. www.morphosource.org/media/000072844

Stanley, E. L., Ceríaco, L. M. P., Bandeira, S., Valerio, H., Bates, M. F., & Branch, W. R. (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.

Stanley, E. L., & Florida Museum of Natural History. (2018). *Cabassous chacoensis (uf:mammals:20650 | ark:/87602/m4/M40499)*. www.morphosource.org/media/000040499

Stanley, E. L., & Yale Peabody Museum. (2018). *Acomys cahirinus* (ypm:vz:mam 5794 | ark:/87602/m4/M64826). www.morphosource.org/media/000064826

Stapp, C. (2022). *Defensive diversity: Factors influencing the interspecific variation in the armor of armadillos (Cingulata)*. California State University.

Strahm, M. H., & Schwartz, A. (1977). Osteoderms in the anguid lizard subfamily Diploglossinae and their taxonomic importance. *Biotropica*, **9**, 58–72.

Stundl, J., Martik, M. L., Chen, D., Raja, D. A., Franěk, R., Pospisilova, A., Pšenička, M., Metscher, B. D., Braasch, I., Haitina, T., Cerny, R., Ahlberg, P. E., & Bronner, M. E. (2023). Ancient vertebrate dermal armor evolved from trunk neural crest. *Proceedings of the National Academy of Sciences of the United States of America*, **120**, 2017.

Tew, M. (2023). *Neural crest cell migration and developmental origin of bony scutes in white sturgeon (Acipenser transmontanus)*. California State Polytechnic University, Humboldt.

Tucker, A. D. (1997). Validation of skeletochronology to determine age of freshwater crocodiles (*Crocodylus johnstoni*). *Marine and Freshwater Research*, **48**, 343.

Vanhooydonck, B., Meulepas, G., Herrel, A., Boistel, R., Tafforeau, P., Fernandez, V., & Aerts, P. (2009). Ecomorphological analysis of aerial performance in a non-specialized lacertid lizard, *Holaspis guentheri*. *The Journal of Experimental Biology*, **212**, 2475–2482.

Vickaryous, M., Willan, G., Williams, C., Kirby, A. C., Herrel, A., Kéver, L., Marghoub, A., Rai, S., Abzhanov, A., Stanley, E., Evans, S., & Moazen, M. (2023). Skeletal diversity in the skin: Histological variation and the evolution of lizard osteoderms. In *International congress of vertebrate morphology* (pp. 221–222). The Anatomical Record.

Vickaryous, M. K., & Hall, B. K. (2006). Osteoderm morphology and development in the nine-banded armadillo, *Dasypus novemcinctus* (Mammalia, Xenarthra, Cingulata). *Journal of Morphology*, **267**, 1273–1283.

Vickaryous, M. K., & Hall, B. K. (2008). Development of the dermal skeleton in *Alligator mississippiensis* (Archosauria, Crocodylia) with comments on the homology of osteoderms. *Journal of Morphology*, **269**, 398–422.

Vickaryous, M. K., Meldrum, G., & Russell, A. P. (2015). Armored geckos: A histological investigation of osteoderm development in *Tarentola* (Phyllodactylidae) and *Gekko* (Gekkonidae) with comments on their regeneration and inferred function. *Journal of Morphology*, **276**, 1345–1357.

Vickaryous, M. K., & Sire, J.-Y. (2009). The integumentary skeleton of tetrapods: Origin, evolution, and development. *Journal of Anatomy*, **214**, 441–464.

Vickaryous, M. K., Williams, C., Willan, G., Kirby, A., Herrel, A., Kever, L., Moazen, M., Marghoub, A., Rai, S., Abzhanov, A., & Evans, S. (2022). Histological diversity and evolution of lizard osteoderms. *The FASEB Journal*, **36**, 2022.

Vidal, D., Ortega, F., Gascó, F., Serrano-Martínez, A., & Sanz, J. L. (2017). The internal anatomy of titanosaur osteoderms from the upper cretaceous of Spain is compatible with a role in oogenesis. *Scientific Reports*, **7**, 42035.

Vitt, L. J., & Caldwell, J. P. (2014). *Herpetology: An introductory biology of amphibians and reptiles* (4th ed.). Academic Press.

von Goethe, J. W. (1817). Bildung und Umbildung organischer Naturen. In *Zur morphologie*(pp. 201–211). J. G. Cotta'scher Verlag.

von Koenigswald, W., & Storch, G. (1983). *Pholidocercus hassiacus*, ein Amphilemuride aus dem Eozän der Grube Messel bei Darmstadt (Mammalia, Lipotyphla). *Senckenbergiana Lethaea*, **64**, 447–495.

Wang, B., Yang, W., Sherman, V. R., & Meyers, M. A. (2016). Pangolin armor: Overlapping, structure, and mechanical properties of the keratinous scales. *Acta Biomaterialia*, **41**, 60–74.

Wang, W., Li, C., Scheyer, T. M., & Zhao, L. (2019). A new species of *Cyamodus* (Placodontia, Sauropterygia) from the early late Triassic of south-west China. *Journal of Systematic Palaeontology*, **17**, 1457–1476.

Warren, D. E., & Jackson, D. C. (2008). Lactate metabolism in anoxic turtles: An integrative review. *Journal of Comparative Physiology. B*, **178**, 133–148.

Watharow, S. (2011). *Living with snakes and other reptiles*. CSIRO Publishing.

Watson, G. F. (1993). *Fauna of Australia – Volume 2A Amphibia and Reptilia*. Australian Government Publishing Service.

Weiss, L. P., & Wislocki, G. B. (1956). Seasonal variations in hematopoiesis in the dermal bones of the nine-banded armadillo. *The Anatomical Record*, **126**, 143–163.

Westheide, W., & Rieger, R. (2015). *Spezielle Zoologie. Teil 2: Wirbel- oder Schädeltiere* (3rd ed.). Springer Berlin Heidelberg.

Wheeler, D. E., & Hölldobler, B. (1985). Cryptic phragmosis: The structural modifications. *Psyche*, **92**, 337–353.

Wheeler, W. M. (1927). The physiognomy of insects. *The Quarterly Review of Biology*, **2**, 1–36.

Whiteside, B. (1922). The development of the saccus endolymphaticus in *Rana temporaria* Linné. *The American Journal of Anatomy*, **30**, 231–266.

Willan, G. Y. (2024). *Histological heterogeneity: Tissue-level diversity of lizard osteoderms*. University of Guelph.

Williams, C., Kirby, A., Marghoub, A., Kéver, L., Ostashevskaya-Gohstand, S., Bertazzo, S., Moazen, M., Abzhanov, A., Herrel, A., Evans, S. E., & Vickaryous, M. K. (2021). A review of the osteoderms of lizards (Reptilia: Squamata). *Biological Reviews*, **12**, brv.12788.

Witmer, L. M. (1995). The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In J. J. Thomason (Ed.), *Functional morphology in vertebrate paleontology* (pp. 19–33). Cambridge University Press.

Witzmann, F. (2009). Comparative histology of sculptured dermal bones in basal tetrapods, and the implications for the soft tissue dermis. *Palaeodiversity*, **2**, 233–270.

Witzmann, F. (2011). Morphological and histological changes of dermal scales during the fish-to-tetrapod transition. *Acta Zoologica*, **92**, 281–302.

Witzmann, F. (2016). CO_2-metabolism in early tetrapods revisited: Inferences from osteological correlates of gills, skin and lung ventilation in the fossil record. *Lethaia*, **49**, 492–506.

Witzmann, F., & Soler-Gijón, R. (2010). The bone histology of osteoderms in temnospondyl amphibians and in the chroniosuchian *Bystrowiella*. *Acta Zoologica*, **91**, 96–114.

Wolf, D. (2007). Osteoderm histology of extinct and recent Cingulata and Phyllophaga (Xenarthra, Mammalia): Implications for biomechanical adaptation and systematics. *Hallesches Jahrb. für Geowissenschaften Beiheft*, **23**, 145–151.

Wolf, D. (2008). Osteoderm histology of the Cingulata (Xenarthra, Mammalia): Implications for systematics. *Journal of Vertebrate Paleontology*, **28**, 161A.

Wolf, D., Kalthoff, D. C., & Sander, P. M. (2012). Osteoderm histology of the Pampatheriidae (Cingulata, Xenarthra, Mammalia): Implications for systematics, osteoderm growth, and biomechanical adaptation. *Journal of Morphology*, **273**, 388–404.

Wolniewicz, A. S., Shen, Y., Li, Q., Sun, Y., Qiao, Y., Chen, Y., Hu, Y.-W., & Liu, J. (2023). An armoured marine reptile from the early Triassic of South China and its phylogenetic and evolutionary implications. *eLife*, **12**, 1–31.

Xue, J., Marghoub, A., Bertazzo, S., Evans, S. E., & Moazen, M. (2017). *Biomechanics of osteoderms in a lizard skull – A preliminary finite element study*. In Anatomical society winter meeting, King's College London.

Yang, W., Chen, I. H., Gludovatz, B., Zimmermann, E. A., Ritchie, R. O., & Meyers, M. A. (2013). Natural flexible dermal armor. *Advanced Materials*, **25**, 31–48.

Youngman, N. J., Llinas, J., & Fry, B. G. (2021). Evidence for resistance to coagulotoxic effects of Australian elapid snake venoms by sympatric prey (blue tongue skinks) but not by predators (monitor lizards). *Toxins (Basel)*, **13**, 590.

Zamora-Camacho, F. J., Reguera, S., Rubiño-Hispán, M. V., & Moreno-Rueda, G. (2014). Effects of limb length, body mass, gender, gravidity, and elevation on escape speed in the lizard *Psammodromus algirus*. *Evolutionary Biology*, **41**, 509–517.

Zangerl, R. (1969). The turtle shell. In C. Gans, A. d.' A. Bellairs, & T. S. Parsons (Eds.), *Biology of the Reptilia – volume 1: morphology A* (pp. 311–339). Academic Press.

Zylberberg, L., & Castanet, J. (1985). New data on the structure and the growth of the osteoderms in the reptile *Anguis fragilis* L. (Anguidae, Squamata). *Journal of Morphology*, **342**, 327–342.

Zylberberg, L., Castanet, J., & de Ricqlès, A. (1980). Structure of the dermal scales in Gymnophiona (Amphibia). *Journal of Morphology*, **165**, 41–54.

Zylberberg, L., & Wake, M. H. (1990). Structure of the scales of *Dermophis* and *Microcaecilia* (Amphibia: Gymnophiona), and a comparison to dermal ossifications of other vertebrates. *Journal of Morphology*, **206**, 25–43.