



The macroevolutionary and developmental evolution of the turtle carapacial scutes

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Eduardo Ascarrunz¹, Marcelo R. Sánchez-Villagra²

¹ Department of Geosciences, University of Fribourg, Chemin du Musée 6, 1700 Fribourg, Switzerland

² Palaeontological Institute and Museum, University of Zurich, Karl-Schmid-Strasse 4, 8006 Zurich, Switzerland

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Corresponding author: Eduardo Ascarrunz (eascarrunz.science@mailfence.com), Marcelo R. Sánchez-Villagra (m.sanchez@pim.uzh.ch)

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Abstract

The scutes of the carapace of extant turtles exhibit common elements in a narrow range of topographical arrangements. The typical arrangement has remained constant since its origin in the clade Mesochelydia (Early Jurassic), after a period of apparent greater diversity in the Triassic. This contribution is a review of the development and evolutionary history of the scute patterns of the carapace, seen through the lens of recent developmental models. This yields insights on pattern variations in the fossil record. We reinterpret the “supracaudal” scute and propose that *Proganochelys* had five vertebral scutes. We discuss the relationship between supramarginal scutes and Turing processes, and we show how a simple change during embryogenesis could account for origin of the configuration of the caudal region of the carapace in mesochelydians. We also discuss the nature of the decrease in number of scutes over the course of evolution, and whether macroevolutionary trends can be discerned. We argue that turtles with complete loss of scutes (e.g., softshells) follow clade-specific macroevolutionary regimes, which are distinct from the majority of other turtles. Finally, we draw a parallel between the variation of scute patterns on the carapace of turtles and the scale patterns in the pileus region (roof of the head) of squamates. The size and numbers of scales in the pileus region can evolve over a wide range, but we recognized tentative evidence of convergence towards a typical configuration when the scales become larger and fewer. Thus, typical patterns could be a more general property of similar systems of integumentary appendages.

Keywords

canalization, ontogeny, pholidosis, scales, Squamata, Testudines, variation

Introduction

A conspicuous feature of amniotes is the diversity of skin appendages that cover their bodies, such as hair in mammals, feathers in birds, and scales in reptiles (including the legs of birds). These appendages have been found to

develop in the embryo from specialized plate-like patches of thickened epidermis, called placodes (Oliveira-Martinez et al. 2003; Milinkovitch et al. 2013; Biggs and Mikkola 2014; Di-Poi and Milinkovitch 2016). The spa-

tial distribution of these placodes during embryogenesis is largely reflected in the distribution of the skin appendages in the body of the adult. Physical processes may also have a major role in the resulting morphological patterns (Milinkovitch et al. 2013). The resulting patterns are of great interest to zoologists. For instance, in squamates, the arrangement of scales is a character complex widely used in species delimitation and identification (e.g. Cope 1886; Campbell and Frost 1993; Weinell et al. 2019). In the herpetological literature, these scale mosaics are variously called pholidosis or scalation. When scales form large shield-like plates called scutes (from the Latin *scutum*, meaning “shield”) contiguous to each other, the mosaic patterns are also called scutation, or scutellation.

Here, we review different aspects of an outstanding example of evolutionarily conserved pholidosis: the mosaic of scutes of the carapace of the dorsal shell of turtles (carapace). It is a rare opportunity to be able to study the evolutionary history of patterns of epidermal appendages in deep time with abundant palaeontological data, and the turtle shell probably provides the best material of this kind.

The first known turtles with a carapace (turtles with a carapace = clade Testudinata; crown turtles = clade Testudines) are from the Late Triassic (Norian, 227–208 Ma) (Scheyer et al. 2013; Joyce 2017; Rieppel 2017). The carapace soon experienced a major change between then and the Early Jurassic (Hettangian, 201–199 Ma). After that phase, the evolutionary history of the pholidosis of the carapace (and plastron) in the majority of turtles has seen mostly minor innovations. Yet, there is substantial intra-specific variation of pholidotic patterns in turtles (Zangerl and Johnson 1957; Bujes and Verrastro 2007; Zimm et al. 2017; Szczygielski et al. 2018; Horváth et al. 2020; Maffucci et al. 2020; Bentley et al. 2021).

In this contribution we integrate a series of recent studies in palaeontology and developmental biology, including a model based on reaction-diffusion processes (Moustakas-Verho et al. 2014), to shed new light on ancient fossils and the constructional factors that have shaped the evolution of the carapace since the earliest known testudinans.

We focus our discussion in the carapace, as the development of the plastron (ventral portion of the shell) has not been studied in similar detail. The developmental systems of scute patterning on the carapace and plastron are considered independent (Cherepanov 2014; Moustakas-Verho and Cherepanov 2015; Cherepanov et al. 2019), but with similarities (Cherepanov 2006; Moustakas-Verho et al. 2014).

The extant turtle carapace and its scute arrangement

Both carapace and plastron are made up of an internal layer of bone plates with contributions of the ribs, and an external layer of scutes. Secondly, the leatherback

sea turtle *Dermochelys coriacea*, the soft-shelled turtles (Trionychidae) and *Carettochelys insculpta* do not have scales on the carapace. Soft-shelled turtles are particularly divergent in their shell and its mode of development (Nagashima et al. 2012, Nagashima et al. 2014, Rice et al. 2015).

Excepting the hawksbill sea turtle *Eretmochelys imbricata*, there is little or no overlap between scutes. The limits between adjacent scutes form epidermal furrows termed seams, following the terminology proposed by Kordikova (2002). Each seam almost always leaves a corresponding impression on the underlying bone plates, known as a sulcus, but these may also disappear in very old adults. Thanks to the sulci it is possible to know the pholidosis of the carapace in the fossil record, despite the keratinous scutes themselves not being preserved along with the bone.

The bone plates and scute mosaic of the carapace of the vast majority of modern turtles conform to a basic plan that appeared in the clade Mesochelydia (Joyce 2017), at least as early as in the Hettangian (Early Jurassic, 201–145 Ma) (Fig. 1). This clade includes nearly all turtles known from the Jurassic to the present. The pholidotic pattern of the “mesochelydian plan” is well demonstrated for the Lower Jurassic turtle *Kayentachelys aprix* (Gaffney et al. 1987) (Fig. 1, Fig. 2), and can be summarized as follows: a small scute called the cervical occupies the antero-medial border of the carapace. Posterior to it there is a series of five scutes called vertebrals, arranged along the midline. A pair of series of four scutes called pleurals are located to each side of the vertebrals. A third series is made up by the marginal scutes, 12 on each side, which are distributed along the rim of the carapace. The twelfth marginal scutes contact each other posterior to the fifth vertebral, forming together with the cervical an outer ring of scutes that surrounds the vertebrals and the pleurals. Throughout this text we will use Roman numerals to refer to the individual scutes in the mesochelydian plan, numbered from anterior to posterior. We also use Roman numerals to refer to the specific scutes of species or specimens where they can be considered *prima facie* homologous to the corresponding scute in the ancestral mesochelydian plan.

The underlying bone plates follow a similar arrangement that is however non-congruent with the scute pattern (Fig. 2). The antero-medial bone plate is called the nuchal, and it is followed by a longitudinal series of typically eight neural plates that develop in part from periosteal expansion of the neural arches of the corresponding trunk vertebrae (Gilbert et al. 2001; Scheyer et al. 2008). Posterior to the neurals there are typically one to three suprapygal plates, followed by the pygal plate that caps the postero-medial border of the carapace. Lateral to each neural there is a pair of costal plates, that develop from the corresponding trunk ribs by periosteal expansion and metaplastic dermal ossification (Gilbert et al. 2001). Finally, eleven pairs of peripheral plates form the lateral rims of the carapace, encircling the neurals, pleurals, and suprapygals. The tip of the ribs associated to each costal fit inside a socket in the nearest peripheral plate.

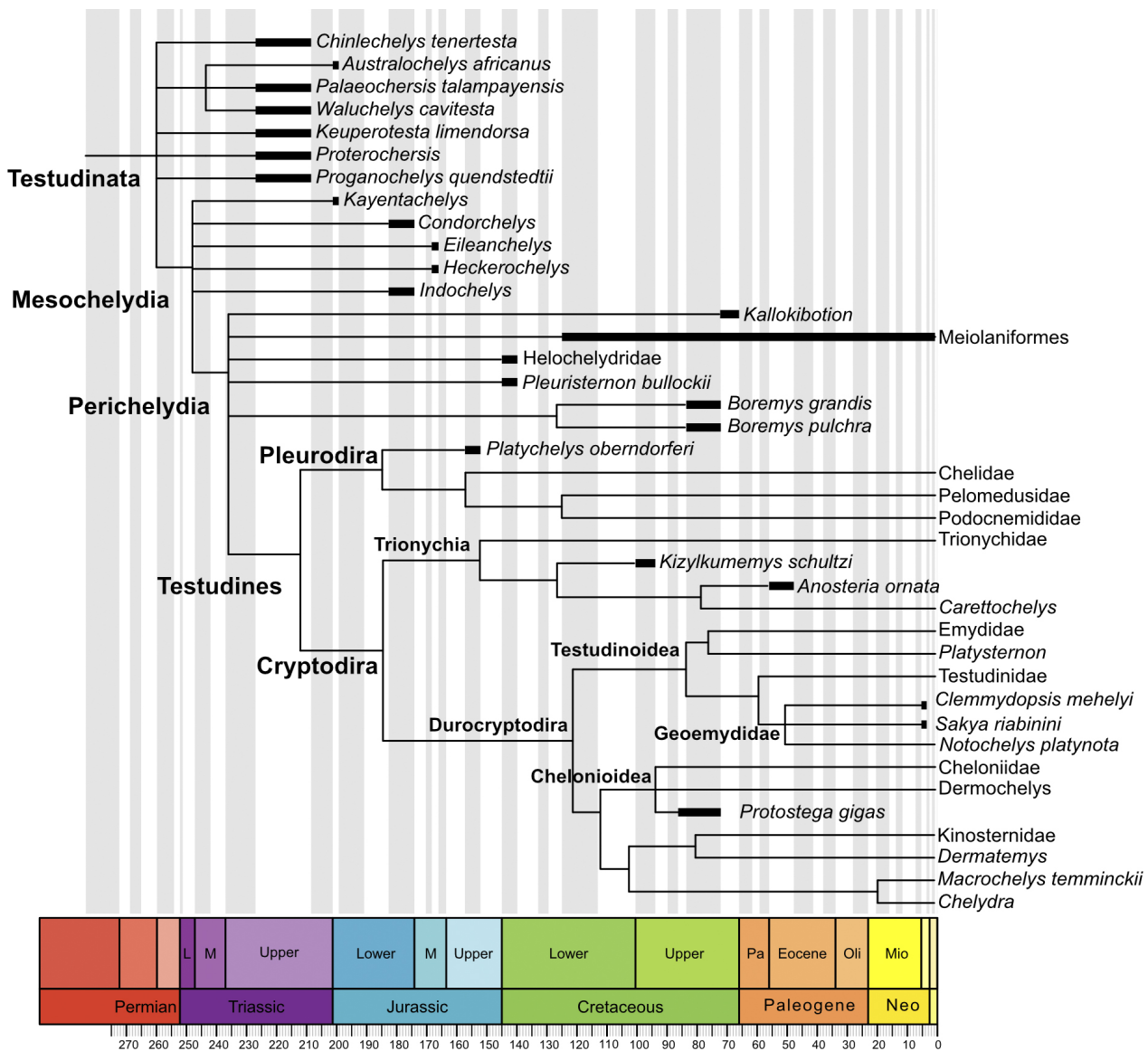


Figure 1. Synthetic phylogeny of testudinans highlighting many of the species and clades mentioned in the text. Based mainly on Joyce (2017), Sterli et al. (2021), and Thomson et al. (2021). Ages of divergences between extant groups are based on the estimates of Thomson et al. (2021). The stratigraphic spans of extant species and clades are not depicted. The ages of the nodes that are directly ancestral to extinct species are arbitrary.

Development of the scute mosaic

The following account synthesizes findings from Cherepanov (1992, 2006, 2016), Gilbert et al. (2001), and Moustakas-Verho et al. (2014) based on the emydids *Trachemys scripta* and *Emys orbicularis*, and the testudinid *Testudo graeca*. The precise timing of the events is difficult to give, because in addition to slight intraspecific and interspecific variations, authors have described the events variously in relation to incubation days, carapace length, or tabled developmental stages (Yntema 1968).

The major feature in the early development of the carapace are the “carapacial ridges”: two nearly parallel longitudinal bulges between the anterior and posterior limb buds, in the flanks of the dorsal region of the embryo (Burke 1989). Along each carapacial ridge are found

the primordia of the marginal scutes, visible as placodes in the invaginations of the transverse myosepta of trunk. Similarly, the placodes of the four pleural scutes appear dorsal to each carapacial ridge, at about the level of the neural tube (Cherepanov 2006). Around the same time, in most turtles the tips of the cartilaginous ribs enter the carapacial ridge, where they become “ensnared”, deflecting their growth into the dorsal dermis (Gilbert et al. 2001; Rice et al. 2015). In trionychids, the carapacial ridge may act differently: it truncates the lateral growth of the ribs (Nagashima et al. 2012; Sánchez-Villagra et al. 2009). Both mechanisms result in preventing growth of the ribs into the ventrum of the embryo, which normally occurs in other vertebrates. The latter is a crucial step in the conformation of the overall structure of the carapace.

In subsequent stages of turtle carapace development, a series of six pairs of placodes appears along the mid-

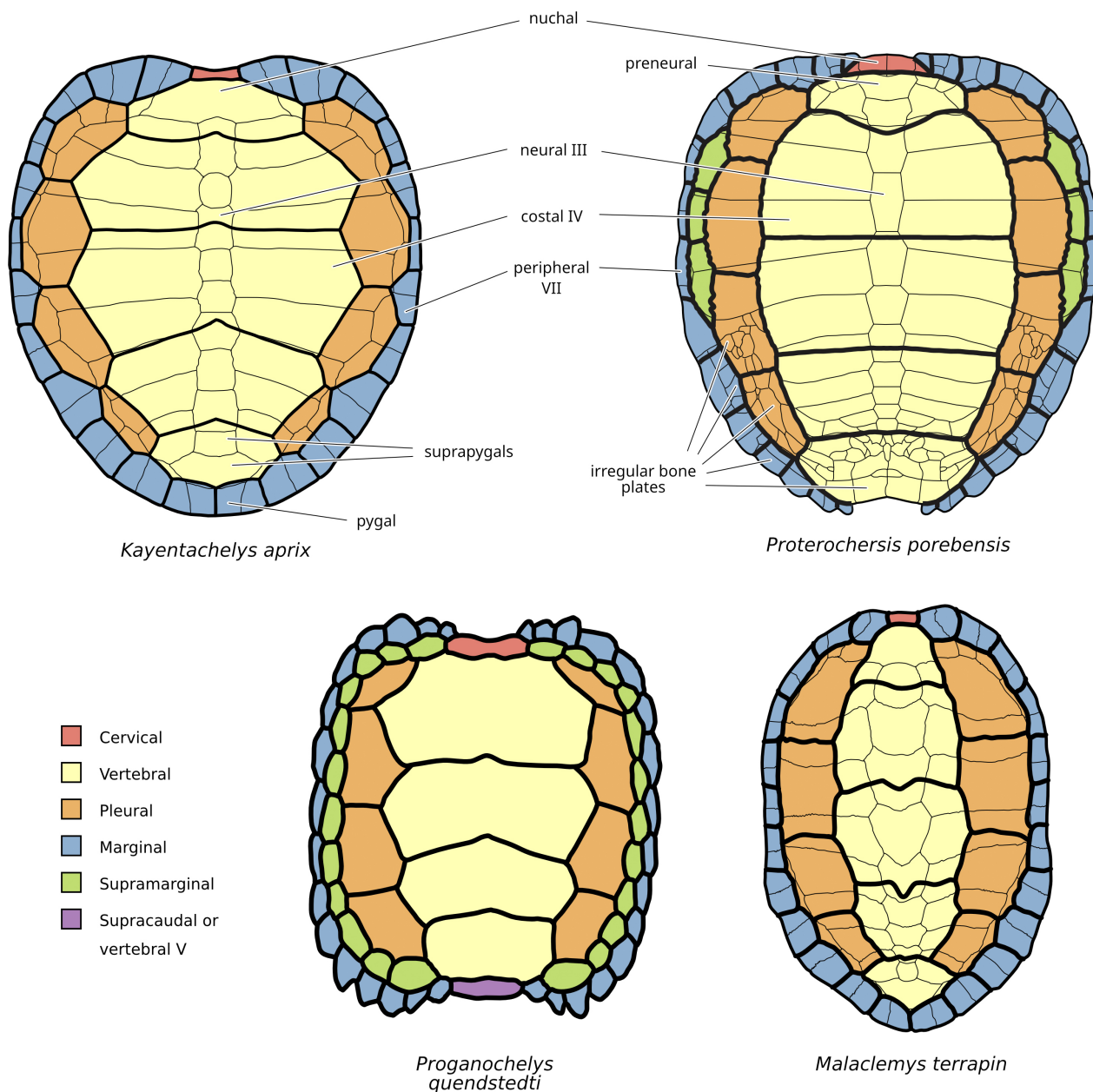


Figure 2. The external anatomy of the bony carapace of testudinatan. Pholidosis is shown by the imprints (sulci) left by the borders of the corneous scutes. *Kayentachelys aprix* is the oldest known testudinatan that displays the complete mesochelydian plan: the general layout of bone plates and scutes that is preserved in the majority of living turtles, such as the emydid *Malaclemys terrapin*. Earlier testudinatan like *Proganochelys quenstedtii* and *Proterochersis porebensis* (reconstructions) had more capacial scutes, and the series of marginal scutes did not meet in the posterior part of the carapace. *Proterochersis* also shows evidence of numerous irregular bone plates that are not present in mesochelydians; see Szczygielski & Sulej (2019) for details. Labelled elements are bone plates. Scute homologies are colour-coded. Thin lines represent bone plate sutures; thick lines represent sulci. The sutures in *Proganochelys* are unknown. *Proganochelys* after Gaffney (1990), *Proterochersis* after Szczygielski & Sulej (2019), *Kayentachelys* after Joyce (unpublished), *Malaclemys* by E.A.

line, on the dorsum of the trunk of the embryo. The five posterior pairs of placodes are the primordia of the five vertebral scutes, and the anterior pair are the primordia of the cervical scute (Cherepanov 2006; Moustakas-Verho et al. 2014). Over the course of this process, the trunk of the embryo experiences significant lateral growth, especially in its middle and anterior regions, and so the elliptical outline of the carapace begins to take shape. Eventually, the primordia of all the scutes begin to expand, and as they do so, the paired primordia

of the vertebral scutes merge. Concurrently, the anterior and posterior ends of the the carapacial ridges extend toward the midline, so that the left and right carapacial ridges contact each other at the posterior end of the trunk, with the primordia of the left and right marginal XII directly posterior to the primordium of vertebral V. The anterior ends of the carapacial ridges end up abutting the primordia of the cervical scute, which around this time begin to fuse. After these events, the general layout of the scutes of the carapace is in place, with

an outer ring formed by the marginals and the cervical scute primordium.

The formation of the seams between the scutes has been described in detail by Cherepanov (1992), based on *Emys orbicularis* and *Testudo graeca*. The epidermis of the postero-lateral border of each vertebral and marginal scute primordia sinks sharply into the dermis, forming the first seams. Soon the same happens with the pleural primordia. The seams then proceed to expand and entirely delimit each scute.

The identities of all the carapacial scutes are thus settled, and their subsequent development is mostly concerned with changes in their proportions and further maturation of the epithelium (Alibardi and Dipietrangelo 2005). It is only around this time that the bony layer of the carapace begins to ossify, starting with the nuchal plate (Gilbert et al. 2001; Sánchez-Villagra et al. 2009), followed by the costals, and much later by the peripherals. The ossifications of the pygal and suprapygals have not been studied in detail, but begin to occur last, around the time of hatching (*Emys orbicularis*; Cherepanov 1992) or, more commonly, months later (Gilbert et al. 2001; Cordero 2021). The scute layer might influence the morphogenesis of the bone plates. Cherepanov (1992, 2019) noted that the seams between the marginal scutes seem to act as organization centres for the osteogenesis of the peripheral plates, by altering the local arrangement of the subjacent collagen fibres in the dermis. Indeed, in virtually all turtles (with no exceptions noted by us in the literature or in our previous experience with specimens) the intermarginal sulci fall near the middle of each peripheral plate, and this coincidence is particularly striking in hatchlings. A similar morphogenic interaction between the posterior intermarginal seam and the pygal is plausible, although to our knowledge this has not been investigated. Similar correspondences between costal plates and interpleural seams have only been reported for the Testudinidae (Procter 1922; Cherepanov 2019).

Models of scute patterning

The turtle carapace provided one of the many examples that D'Arcy Thompson (1942) used in his landmark book *On Growth and Form*, seeking explanations of biological forms in terms of mathematical and physical processes. He classed the pholidosis of the carapace in a category of typically hexagonal tessellations that emerge as neighbouring elements squeeze each other due to divergent radial forces from within (in this case growth) or under the influence of uniform external forces. This notion does not account for the number and location of scute primordia, but remains a feasible and simple explanation for the roughly polygonal shapes, and is compatible with the more modern and detailed models that we describe below. It is likely that other authors unknown to us (e.g. Russian researchers writing in their own language) also pioneered

attempts to explain the development of the pholidosis of the turtle carapace.

Over the course of the last few decades, Cherepanov and colleagues (Cherepanov 1992, 2006, 2015, 2016; Moustakas-Verho and Cherepanov 2015; Cherepanov et al. 2019) have put forward a segment-dependent model for the patterning of carapacial scutes, based primarily on histological sections of embryos and variation data. The model posits a strict correspondence between the scute placodes and thoracic myosepta. Specifically, in the standard mesochelydian plan the twelve marginal scute placodes develop in the pits of thoracic myosepta I to XII. In the most recent version of the model (Cherepanov et al. 2019), the placodes of the vertebral scutes develop at even-numbered myosepta, and the placodes of pleural scutes develop at odd-numbered myosepta, laying down the staggered pattern that is recognizable in the fully developed scutes. In the model, the association between scute placodes and myosepta also holds for deviations from the mesochelydian plan. When present, the segment-dependent model predicts that additional vertebral or pleural scute placodes appear occupying normally vacant regions of thoracic myosepta, or associated to new body segments added to the trunk. Adult scute patterns consistent with that prediction were found in the natural variation of pholidotic patterns in *Lepidochelys olivacea* (Cherepanov et al. 2019), and in abnormal pholidotic patterns in *Testudo graeca* and *Emys orbicularis* (Cherepanov 2014).

A causal model to explain the generation of scute patterns based on Turing patterns was introduced by Moustakas-Verho et al. (2014). A notable success in developmental biology was the introduction of mathematical models of reaction-diffusion processes by Turing (1952; Gierer and Meinhardt 1972). In their simplest form, these models describe the patterns created by the interaction of a pair of molecular agents acting as activator and inhibitor diffusing in the same medium. The activator increases the synthesis of both itself and an inhibitor, while the inhibitor suppresses the synthesis of the activator and diffuses at a higher rate. The local concentration patterns of the two molecular actors can create the so-called Turing patterns, which reproduce a variety of biological patterns, including the distribution and colouration patterns of skin appendages (Fofonjka and Milinkovitch 2021). Classical examples include the formation of spots, stripes, and labyrinths. Examples of molecular species that could act as activator-inhibitor pairs have been identified in various biological patterning systems, including the development of pholidosis in different amniotes.

The model of Moustakas-Verho et al. (2014) consists of a first reaction-diffusion process that defines the location of the scute placodes, coupled with a second reaction-diffusion process with a different pair of activator and inhibitor species. The second process describes how the primordia grow and fill the surface of the carapace. The model was implemented in a computer simulation where diffusion occurs in a rectangular grid that represents the epidermal epithelium of the trunk of the embryo. A single cell in the grid can be taken to represent a small patch

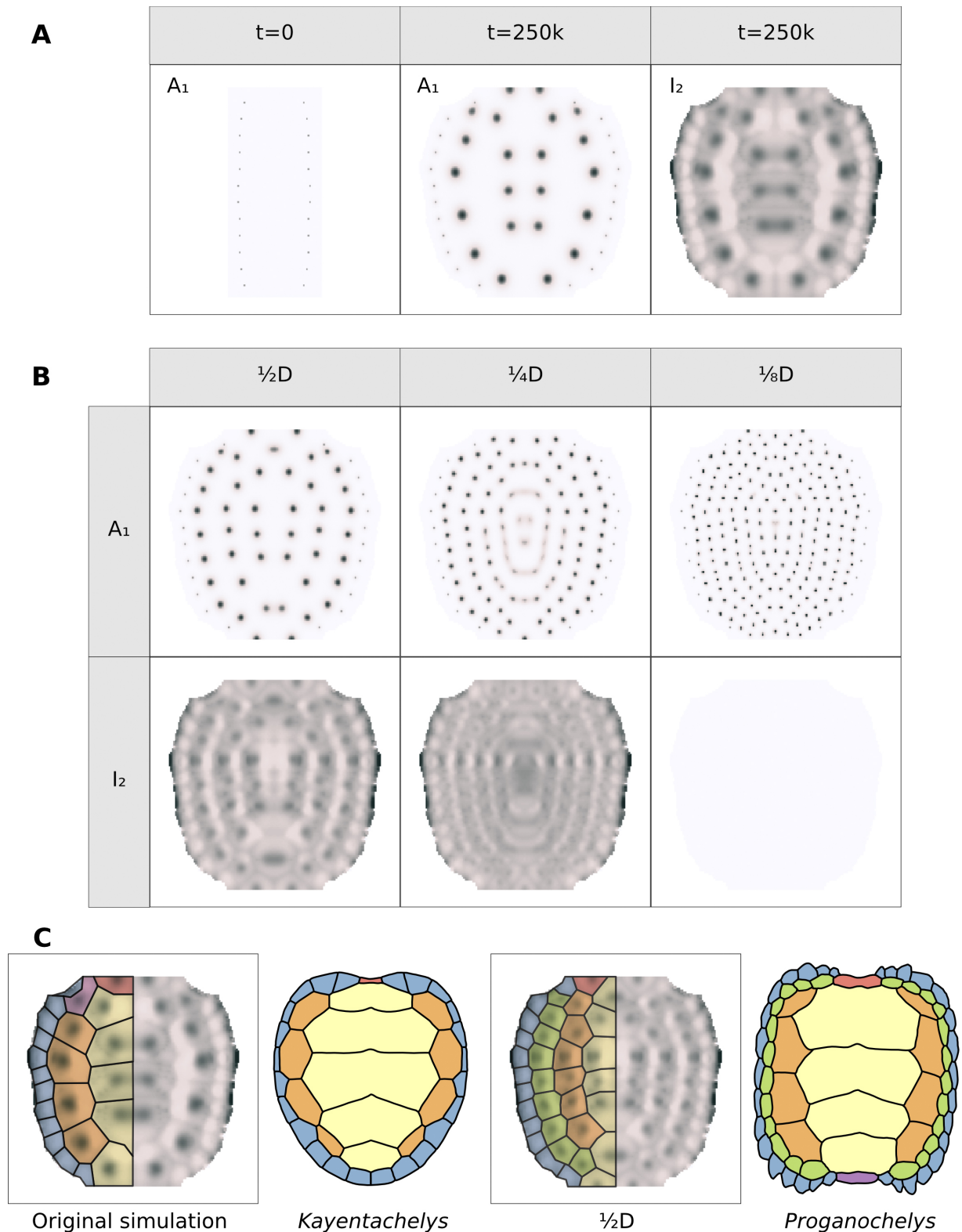


Figure 3. Simulations of pholidosis of the carapace with a reaction-diffusion model. Darker colours indicate higher concentrations of activator of the first reaction diffusion-process (A₁) or the inhibitor of the second reaction-diffusion process (I₂). A, The beginning (t=0) and end (t=250000 iterations) of the simulation with the original parameters of Moustakas-Verho et al. (2014). The diffusion rates of A₁ and its inhibitor I₁ are 4 and 120, respectively. B, Simulations with lower diffusion rates of the activator and the inhibitor in the first process. The simulation with $\frac{1}{8}$ of original diffusion rate parameters was run for 300000 iterations, and formed additional series of placodes but not scute seams. C, Comparison of simulated and real pholidosis patterns.

of cells in the epidermis. The initial state of the model defines the chemico-kinetic properties of the activators and inhibitors, and a pre-pattern of the early location of

the 12 marginal placodes along the two carapacial ridges (Fig. 3A). Additional parameters describe simple lateral growth of the thorax, its acceleration, and the timing of

the onset and termination of the reaction-diffusion processes. The extension of the ends of the carapacial ridge toward the midline is not modelled.

This relatively simple model is highly successful in reproducing key features of the scute mosaic. The first reaction-diffusion process originating from the twelve pairs of marginal placodes induce the formation of two rows of four or five “pleural” placodes, and a medial row of six pairs of placodes representing the cervical and the five vertebrals. The second reaction-diffusion process mimics the growth of the primordia and the appearance of the scute seams. The result is most satisfactory in the middle region of the trunk, even reproducing the fusion of the pairs of primordia of vertebrals II, III, and IV (Fig. 3C).

The model was also successful in replicating abnormal scute patterns of actual turtles (Moustakas-Verho et al. 2014, Zimm et al. 2017). Furthermore, Moustakas-Verho et al. (2014) performed protein-soaked bead implantation experiments in embryos of *Trachemys scripta* that allowed them to identify *Shh* and *FGF4* as likely molecular morphogenetic agents that may be acting as activator and inhibitor during the first reaction-diffusion process.

The reaction-diffusion model provides a causal complement to the general thrust of the segment-dependent model. This is particularly relevant because, beyond the pre-pattern of twelve marginal placodes along the carapacial ridges, the reaction-diffusion model involves no concept of body segmentation. Still, it has not been explored to what extent the reaction-diffusion model can reproduce the range of intraspecific supernumerary scale variations that are strongly suggestive of the strict correspondence between myosepta and scute placodes (Cherepanov et al. 2019). Moustakas-Verho et al. (2014) showed that axial elongation of the trunk under the reaction-diffusion reproduces a patterns of supernumerary pleurals and vertebrals, as is present in *Lepidochelys olivacea*. Many other patterns recorded for this species also feature supernumerary marginal scutes, which in theory represent supernumerary body segments. In any case, an explanatory bridge between the two models remains to be completed. It is possible that the transversal invaginations that mark each thoracic myoseptum participate in the reaction-diffusion process, acting as zones that facilitate the accumulation of the first activator morphogen either due to the infolding of the myosepta or due to local biochemical interactions.

Revisiting basal testudinians

There are only eight known and undisputed species of non-mesochelydian turtles, most of them from the Norian (Late Triassic, 227–208.5 Ma; except *Australochelys africanus* from the Hettangian) (Fig. 1), we refer to them in this text as “basal testudinians”. The pholidosis of the carapace of only a few of those species is known in sufficient detail to remark on the differences with respect to the mesochelydian plan.

The most complex pholidosis is seen in *Proganochelys quenstedtii* (Fig. 2), in which one cervical, four vertebrals, four pairs of pleurals, and 16 or 17 pairs of marginals are usually recognized. In addition, *Proganochelys* exhibits paired series of 12 supramarginal scutes located between the pleurals and the marginals, and a so-called “supracaudal” scute occupying the caudal edge of the carapace, posterior to the fourth vertebral and flanked by the last marginals (Gaffney 1990). Many authors refer to the scute that in testudinids results from the fusion of the left and right marginal scutes XII as a “supracaudal”. To our knowledge, no author has proposed the homology between the “supracaudal” of basal testudinians and the posteriormost marginals of testudinids.

The almost complete scutation pattern can also be observed in *Proterochersis porebensis* and *Proterochersis robusta*, where there are typically one cervical, five vertebrals, four pairs of pleurals, 14 marginals (at least 12 in *Proterochersis porebensis*), and three supramarginals (Szczygielski and Sulej 2016).

The left and right series of marginal scutes do not meet at the midline in the caudal region of the carapace in any of the earliest testudinians where this condition can be ascertained: *Proganochelys quenstedtii*, *Proterochersis* spp., *Waluchelys cavitesta*, and *Palaeochersis talampayensis* (Gaffney 1990; Rougier et al. 1996; Szczygielski and Sulej 2016; Sterli et al. 2021). Instead, the last marginal scutes flank a wide caudal notch (most authors call this feature a “pygal notch”, but we avoid that term because it is more commonly used to refer to a smaller notch confined to the pygal plate), and the most posterior scute is vertebral V in *Proterochersis* or the “supracaudal” scute in *Proganochelys* and *Waluchelys cavitesta*. This notch occurs approximately in the area of the carapace where the suprapygal and pygal plates are present in mesochelydians, and some authors have argued that therefore it is possible that basal testudinians lacked the full complement of pygal and suprapygal plates (Sterli et al. 2021). Instead, the examination of sutural patterns in specimens of *Proterochersis porebensis* and *Proterochersis robusta* showed that the caudal region of the carapace was made up of an irregular patchwork of osteoderms wherein there are no readily apparent homologues of suprapygals, pygals, and peripherals (Szczygielski and Sulej 2019). Similar irregular sutures have been found in the carapace of *Chinlechelys tenertesta* (Joyce et al. 2009), of which only a few small fragments are known (Szczygielski and Sulej 2019; Lichtig and Lucas 2021).

We propose, first, that the fundamental difference in the development of the caudal region of the carapace of basal testudinians was the failure of the lateral marginal scute series to meet at the midline, posterior to the primordium of vertebral V. It is easy to derive this inference from the fact that in extant turtles the series of marginal scute primordia develop early along the carapacial ridges, when the ridges are roughly parallel to each other, on the flanks of the embryo. Thus, vertebral V remains at the postero-medial edge of the carapace, preserving the relative position of the scute primordia from the early

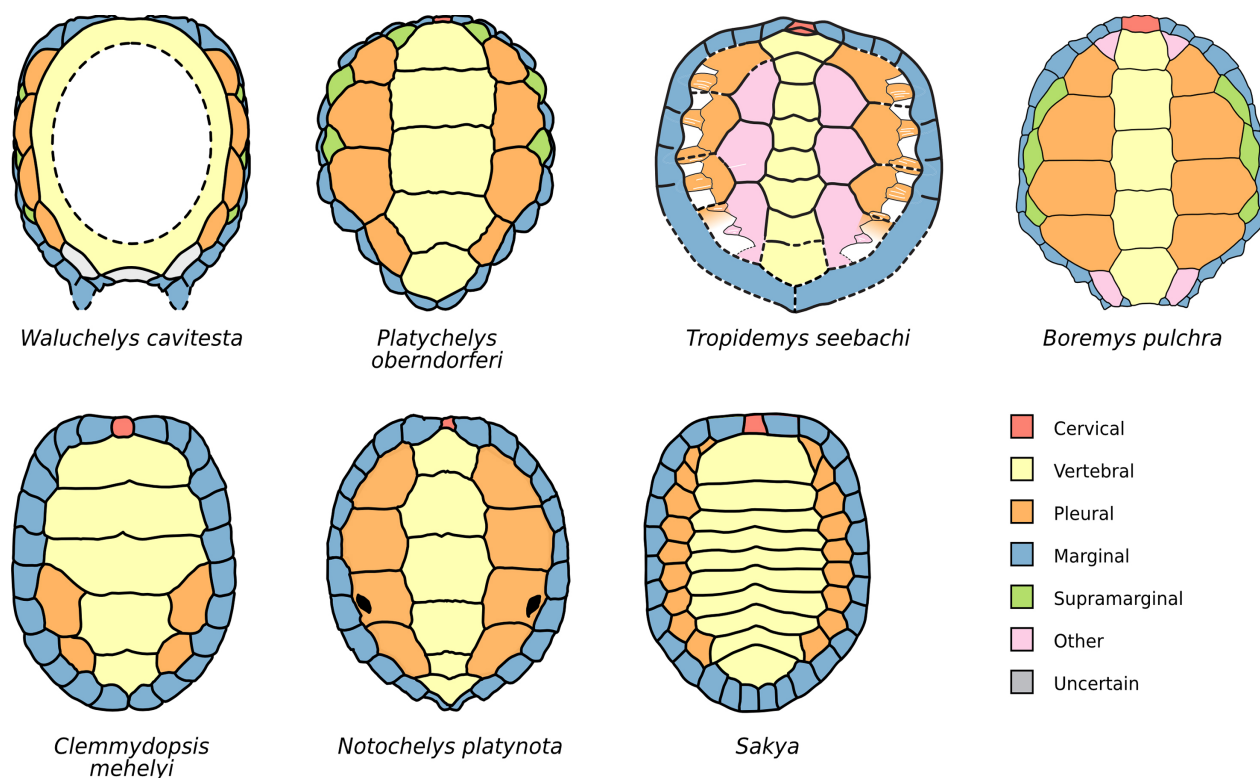


Figure 4. Comparison of the carapace pholidosis of several testudinatans. *Waluchelys cavitesta* after Sterli et al. (2021), *Platycheilus oberndorferi* idealized from Sullivan & Joyce (2017), *Tropidemys seebachi* reconstructed from Joyce & Mäuser (2020), *Clemmydopsis* and *Sakya* after Danilov (2005). The central region of the carapace of *Waluchelys cavitesta* is unknown.

stages of development. This leads us directly to a second proposition: that it might not be necessary to retain the notion of a distinct kind of scute called “supracaudal”, unique to basal testudinatans. Instead, we propose that the “supracaudal” attributed to *Proganochelys* and *Waluchelys* might be a very short vertebral V, with the same topological relations as seen in *Proterochersis*, except with respect to the supramarginals. Embryological observations and the reaction-diffusion model show that the all scutes along the midline of the carapace (the cervical and the vertebrals) have the same initial mode of development from paired placodes (Cherepanov 1992, 2006; Moustakas-Verho et al. 2014; Moustakas-Verho and Cherepanov 2015). The “supracaudal” can also be expected to belong to the same meristic series, based on its position in posterior end of the midline of the carapace. That position in the series of midline scutes in *Proganochelys* indicates identity with vertebral V. The morphology of the “supracaudal” is clearly different from vertebrals I–IV, but it does resemble the morphology of the cervical, which is another specialized scute in the same meristic series. Also like the cervical, and unlike the other vertebrals, the “supracaudal” scute in *Proganochelys* (and apparently *Waluchelys*) does not contact pleural scutes. This condition is, to our knowledge, unprecedented in other turtles, but it does emerge in simulations with the reaction-diffusion model (Fig. 3C; see more details below).

Thus, in our new interpretation, *Proganochelys* has five vertebral scutes, just as *Proterochersis* and the vast majority of mesochelydians. The pholidosis of the cen-

tral region of the carapace of other basal testudinatans is unknown, and in the absence of contradictory evidence, it is reasonable to presume that they also had five vertebral scutes in total.

Another possible interpretation of the nature of the “supracaudal” of basal testudinatans, is that it is the result of the fusion of multiple marginal scutes, and therefore the marginal series meet in the caudal region of the carapace in *Proganochelys* and *Waluchelys*. A fusion of the XIIth pair of scutes occurs in tortoises (Testudinidae), which results in a single scute occupying the posteromedial edge of the carapace (see above) (Joyce and Bell 2004; Cherepanov 2006). However, testudinids do not feature comparable caudal notches, and this alternative interpretation is less parsimonious with respect to the relations of homology. Moreover, there are analogues in other clades that suggest the feasibility of the anatomical configuration that we propose. Among extinct mesochelydians, the cryptodirans *Sinemys* and *Eurysternum wagleri*, and various species in the clade Baenodda (Fig. 4) also display caudal notches (Tong and Brinkman 2013; Anquetin and Joyce 2014; Joyce and Lyson 2015), with vertebral V occupying the postero-medial edge of the carapace and flanked by the left and right series of marginal scutes that do not meet. We posit that those species represent very rare instances of re-evolution of the basal testudinatan caudal region, with a similar developmental origin.

Apart from the caudal notch, another distinctive feature of basal testudinatans is the presence of supramarginal scutes. This is the most difficult series of scutes to

Table 1. Gains and losses of scutes. Minimal (most parsimonious) independently accumulated gains and losses of carapacial scutes apomorphic for selected species or clades of testudinans. The “nuchal scute” (Gaffney 1972) posterior to the cervicals in *Boremys grandis* was coded as a vertebral. This species was chosen as the representative of the Eubaeninae because of its extreme proliferation of putative supramarginals; it is likely that other homoplastic scute gains occurred in the Eubaeninae. An unpaired supracaudal scute has been reported for one specimen of *Platycheilus oberndorferi* (Sullivan and Joyce 2017). Names in parentheses denote more inclusive clades in which gains or losses began to accumulate. Question marks denote cases in which the full scute series is unknown. † Extinct.

Clade or species	Cervicals	Vertebrales	Pleurals (pairs)	Marginals (pairs)	Other (pairs)	Reference
Mesochelydia	0	0	0	–2 to –4	–2 to –12	Joyce 2017
<i>Elseya</i>	–1	0	0	0	0	Ascarrunz, unpublished
Kinosternidae	0	0	0	–1	0	Joyce and Bourque 2016
<i>Lepidochelys olivacea</i> (Caretinae)	0	0 to +2	+1 to +2	+1	0	Cherepanov et al. 2019
<i>Macrochelys</i>	0	0	0	0	+3 to +4	Pritchard 1979
<i>Notochelys platynota</i>	0	+1	0	0	0	Brophy and Ernst 2004
Pelomedusoides	–1	0	0	0	0	Ascarrunz, unpublished
<i>Testudo graeca</i> (Testudinidae)	–1	0	0	–1	0	Pritchard 1979
<i>Boremys grandis</i> † (Eubaeninae)	+2	+1	0	0?	+9?	Lively 2016
<i>Clemmydopsis mehelyi</i> †	0	0	–2	0	0	Danilov 2005
<i>Kallokibotion</i> †	–1	0	0	0	0	Pérez-García and Codrea 2018
<i>Naomichelys speciosa</i> †	0	0	0	0	+1	Joyce et al. 2014
<i>Platycheilus oberndorferi</i> †	0	0	0	0	+3	Sullivan and Joyce 2017
Pleurosternidae†	–1	0	0	0	0	Guerrero and Pérez-García 2021
<i>Sakya riabinini</i> †	0	+5	+6	+2	0	Danilov 2005
<i>Tropidemys seebachi</i> † (Thalassochelydia)	+1	+3?	0?	0?	+3?	Joyce and Mäuser 2020
Total gains – losses	–2	+10 to +12	+5 to +6	–1 to –3	+7 to +18	

characterize, as their numbers and anatomical location vary widely across species. In addition to basal testudinans, supramarginal scutes also occur in the alligator snapping turtle *Macrochelys temminckii* (Pritchard 1979; Joyce 2016), and in fossil eubaenines (Joyce and Lyson 2015) and the stem-pleurodire *Platycheilus oberndorferi* (Sullivan and Joyce 2017) (Fig. 4). The reaction-diffusion model can recreate additional longitudinal series of scutes by altering the diffusion area or the diffusion rates of the activator and the inhibitor in the first reaction-diffusion process (Zimm 2019). We explored adjustments with both approaches, and obtained the most satisfactory results by halving the diffusion rates (Fig. 3B), while keeping all the other model parameters identical to the values used by Moustakas-Verho et al. (2014). The control files for reproducing the simulations are provided in the supplementary files. The result roughly approximates the pholidosis of *Proganochelys* (Fig. 3C), but also introduces several supernumerary scutes in the vertebral and pleural series. It might be possible to obtain more realistic results with other parameter combinations, or with further adjustments of the model. However, the location and number of supramarginal scutes is highly variable between species (Fig. 4, Table 1), and likely involve non-homogenous developmental conditions not yet considered. The ideal path for researching supramarginal scutes would be to study of the early development of the carapace in *Macrochelys temminckii*, the only extant species that features supramarginal scutes.

Macroevolutionary patterns, adaptations, and canalization

The evolution of the testudinatan shell from the Triassic to the present has resulted in a net reduction in the average number of its constituent elements. Various authors have thus recognized this as a macroevolutionary trend towards simplification of both the numbers of bony plates and epidermal scutes (Gadow 1899; Newman 1906; Zangerl 1969; Gaffney 1990; Cherepanov 2015; Cordero and Vlachos 2021). Zangerl (1969), for instance, conceived progressively simplified “levels of organization” of the testudinatan shell, which different lineages of turtles would have traversed in parallel.

Here we take a closer look at the history of gains and losses of carapacial scutes. We will first consider the majority of turtles that retain the epidermal scutes. We will address turtles with complete loss of scutes separately.

The modern turtle shell displays a distinctive pholidotic pattern in that a large surface of the body is covered with a mosaic of few scales (typically 38 in the carapace; Fig. 2). We compiled a list of independently accumulated gains and losses of carapacial scutes from basal testudinans to the present (Table 1). The list is not exhaustive. We focused on documenting gains and losses that were unambiguous given the current incomplete knowledge of the phylogeny of testudinans, and in including the most extreme cases. The relationships between basal testudinans are unresolved (Sterli et al.

2021), so we did not count gains or losses among them, and we considered both *Proganochelys quenstedtii* and *Proterochersis robusta* as representing possible ancestral states for counting the losses accumulated along the lineage leading to the Mesochelydia. The list shows that variations with fewer scutes are more widespread among extant species (Testudinidae 65 spp., Pelomedusoides 35 spp., and Kinosternidae 27 spp.; Turtle Taxonomy Working Group 2017). However, when the independently accumulated scute gains and losses are tallied, the gained scutes are more numerous (Table 1). This apparent contradiction results from the extinction of many clades with scute gains, and the great diversification of a few clades with scute losses. But is this historical pattern the result of chance, or are there distinct processes consistently driving this dynamic over macroevolutionary time scales? If so, what are they? Even though the direction and trajectory of the mean number of carapace scutes appears downward in time, the presence of a trend in the sense of a recognizable statistical bias has not been tested. A rigorous approach to these questions ought to make use of comparative phylogenetic methods, which provide means to study hypotheses about macroevolutionary regimes with explicit stochastic models (Ascarrunz et al. 2019). Dynamics that produce within-lineage scute-gaining trends can be characterized with Brownian motion with a bias (called Brownian motion with a trend; Hunt 2006), or Ornstein-Uhlenbeck processes (Harmon 2018). A between-lineage trend toward scute loss can be represented by the SSE (State Speciation and Extinction; Maddison et al. 2007) family of models where the value of a trait (number of scutes) are associated with differential rates of speciation and extinction (Harvey and Rabosky 2018; Herrera-Alsina et al. 2019; Nakov et al. 2019).

Cordero & Vlachos (2021) presented the first quantitative analyses of the evolution of the numbers of shell elements with comparative methods. But they too acknowledge that scute gains and losses represent fairly rare events over the course of the evolutionary history of testudinans, and that it is difficult to sample the relevant species in an unbiased manner. For this reason, the overall rate of change in scute number is bound to be small. If there are statistically identifiable trends in the dominant macroevolutionary regime, they are subtle. Properly characterizing them will require extensive scute number variation data, and a comprehensive time-scaled phylogeny of testudinans. Neither are available at the moment.

Finally, we note that it is difficult to conceive a distinct and plausible mechanism for between-lineage downward trends in scute number. Between-lineage dynamics have been attributed to species selection (Jablonski 2008), where the value of a trait affects the rates of speciation and extinction specific to each lineage. Rather than diversification being affected by gains and losses of scutes, it seems more plausible to assume the presence of unknown developmental factors that increase the liability to scute gain but also have other morphological or physiological effects that decrease fitness or adaptability the population. Cordero & Vlachos (2021) are also hesitant to associate

trends of loss of bone and scute elements of the shell in general with specific mechanisms. Given the paucity of data, these matters are likely to remain in the realm of speculation.

It has been suggested that groups of species in a new “Bauplan” have more variability (i.e., more capacity to generate variation) than subsequent clades, which are less prone to vary (Waddington 1957). This pattern has been associated with “canalization”, defined as “the reduced sensitivity of a phenotype to changes or perturbations in the underlying genetic and nongenetic factors (e.g., the environment) that determine its expression” (Flatt 2005: 288). It is thus hypothesized that morphological variation among species appears before taxonomic diversity (Erwin 2007). As in most other vertebrate clades examined using palaeontological data (Benton et al. 2014), in turtles there seems to be more variation and “morphological experimentation” in the early evolution of the group than in more nested clades as the scute pattern is concerned. An issue that remains to be examined in basal testudinans is that of intraspecific morphological variation in macroevolutionary timescales, and whether it reflects canalization (Pimienta et al. 2018). The limited number of known species and lack of sufficient sampled individuals fail to provide a proper dataset for a quantitative assessment of the matter.

The evolutionary history of testudinans carapacial scutes involved different macroevolutionary regimes. We examine in the following subsections the clades that feature complete loss of shell scutes: Trionychia, and the marine turtles Dermochelyidae and Protostegidae. The developmental processes that produce total loss of scutes (see below) are quite different from the ones that produce the loss of individual scutes, where the total corneous coverage of the shell is preserved by fusions or compensatory expansions of other scutes in a space-filling manner (reviewed in Cherepanov 2015). Also, the resulting external shell skin is unlike the cornified skin of the shell of other turtles. Thus, they are likely linked to developmental and adaptive shifts that delineate distinct macroevolutionary regimes.

Macroevolutionary patterns and adaptations in Trionychia

The clade Trionychia includes the Trionychidae (soft-shell turtles) and Pan-Carettochelys (the scute-less pig-nosed turtle *Carettochelys insculpta* and numerous extinct relatives; Joyce 2014). These are highly aquatic turtles, in which the importance of water-retaining capacity of cornified scutes (Alibardi 2003) is reduced, and there is a physiological advantage in the utilization of the unkeratinized skin on the surface of the shell as a respiratory organ (Scheyer et al. 2007). Trionychids have evolved towards efficient and prolonged extrapulmonary aquatic respiration (Ultsch et al. 1984; Stone et al. 1992), an important part of which can occur through

the skin (ca. 70% for *Trionyx triunguis* in an experimental setting; Girgis 1961). In particular, the skin covering the plastron in the trionychid *Apalone mutica* is much more permeable than the shell scutes and other skin in other aquatic turtles (Dunson 1986). Cutaneous respiration in *Carettochelys* has not been studied directly, but its shell skin is grossly similar to that of trionychids. *Carettochelys* inhabits predominantly normoxic waters, which is consistent with important skin function in gas exchange (Joyce et al. 2012). There are also quantitative similarities in porosity of costal plates of *Carettochelys* and trionychids, which is a proxy for the vascularization associated with cutaneous respiration, but this relationship is not unequivocal (Clarac et al. 2020). Finally, there is significant evidence for parallel adaptation in genes critical to aerobic respiration (oxidative phosphorylation pathway genes) in the mitochondrial genomes of trionychids and *Carettochelys* (Escalona et al. 2017), underscoring the evolutionary importance of physiological modifications of the respiratory systems in the two lineages.

We infer that in early trionychids and the ancestors of *Carettochelys*, scute loss was driven by the adaptive value in the decornification of the skin covering the shell, and a relaxation of the strength of natural selection for the maintenance the developmental system of periodic patterning that determines the scute mosaics. Similar hypotheses have been put forward by previous authors (Scheyer et al. 2007; Nakajima et al. 2017). The fossil record of Pan-*Carettochelys* (Joyce 2014) and trionychids (Georgalis and Joyce 2017) clearly shows that scute losses occurred in parallel, after the divergence of the two clades from their last common ancestor. The ultimate mechanisms by which scute loss is realized in both lineages are also quite different. Juveniles of *Carettochelys insculpta* display rudimentary and apparently unkeratinized scutes on the carapace, with visible seams and an unusual pholidosis of as many as 8 vertebrals, a cervical, and marginals (Zangerl 1959; partially visible in the photographs in Beggs et al. 2000). The scute seams disappear completely by adulthood. Thus, the basic periodic patterning system is retained in *Carettochelys*, although the induced seam pattern has been allowed to drift away significantly from the mesochelydian plan. The transient occurrence of intermarginal seams might be necessary for the development of the peripheral plates, per Cherepanov's (2019) observation that these seams act as organizers of peripheral plate ossification centres (see above). Trionychids, in contrast, have dispensed with both seams and peripherals. Among trionychids, peripheral-like ossicles develop only in *Lissemys* spp., and their homologies are still uncertain (Delfino et al. 2010); all other species completely lack peripheral-like structures. In the trionychid *Pelodiscus sinensis* there is no formation of the initial patterning of marginal scute placodes and the correlated punctuated expression of *Shh*, *Bmp2*, and *Gremlin* along the carapacial ridges, preventing the subsequent induction of the rest of the scute mosaic (Moustakas-Verho et al. 2014).

Macroevolutionary patterns in sea turtles

It is more difficult to hypothesize about the drivers for scute loss in the marine turtle clades Protostegidae and Dermochelyidae. Only the latter is represented by an extant species, the leatherback turtle *Dermochelys coriacea*. The Protostegidae might be stem-chelonioids or the sister clade of Dermochelyidae (Evers and Benson 2019; Evers et al. 2019a); in either case there is palaeontological evidence showing that the loss of scutes occurred independently in both clades (Zangerl 1960; Hirayama and Chitoku 1996; Hirayama 1997). Cutaneous respiration is not a feasible strategy for marine turtles, and for *Dermochelys coriacea* in particular (Escalona et al. 2017). The loss of cornified scutes and subsequent modifications of the shell in dermochelyids might be associated with the origins of many adaptations to life in open sea and deep diving, as seen in living leatherbacks. The lack of a fully rigid shell, particularly in the plastron, probably assists leatherbacks in accomplishing lung collapse during diving (Fossette et al. 2010). The presence of a thick subcutaneous layer of blubber probably also assists deep diving (> 1000 m) by providing thermal insulation, and can serve as a nutrient reserve during long migrations. The elasticity of the uncornified skin allows significant alteration of the thickness of the blubber deposits and overall body shape in response to ecophysiological factors, such as nutrient availability and reproductive status (Davenport et al. 2011). Although those facts alone do not amount to a strong case for diving and thermoregulation as the specific drivers of scute loss, they show that *Dermochelys* displays extensive adaptations to a unique physiology and habitus among living turtles, which may justify the presumption of a distinct evolutionary regime is operating on dermochelyids. The protostegid *Desmatochelys* has enlarged semicircular canals, a feature that is even more pronounced in *Dermochelys coriacea* (Evers et al. 2019b), which could indicate similarities in locomotor behaviour between the two species, although the precise functional implications remain unclear (S. Evers, pers. comm. 2021).

Scales and developmental bias

It is illuminating to seek parallels between character systems in different clades. For the pholidosis of the turtle carapace, though, is difficult to come by with analogous (or homologous) character systems that display relevant similarities in the morphological, developmental, and evolutionary characteristics that we have discussed in this paper. For instance, the large scales on the body of pangolins do not grow in a surface-filling fashion forming a mosaic, as they are arranged in numerous overlapping rows (Wang et al. 2016). Armadillo armour scales are more similar to turtles' in that they do not overlap and

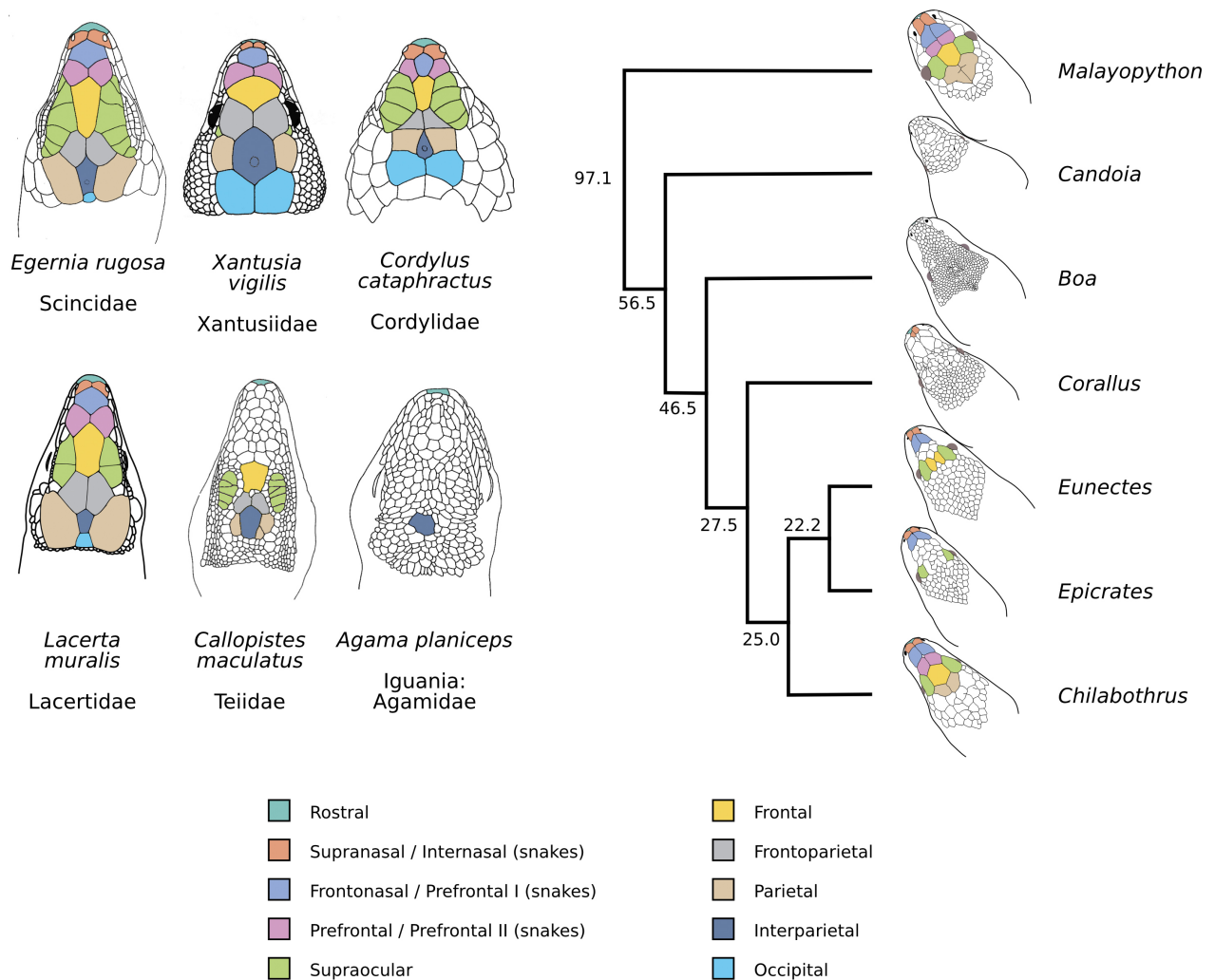


Figure 5. Pileus scalation patterns in squamates. **Left:** Traditionally hypothesized homologies of scales between different squamate clades. Identities become clear only when the scales are large, forming scutes. Diagrams after Ursel (1978) and Gauthier et al. (2008) for *Xantusia*. **Right:** The typical pattern of pileus scutes of snakes appears in the boa *Chilabothrus*, nested in a clade where the likely ancestral condition was with granular scales. The same scutes can be identified in the *Chilabothrus* and the distantly related python *Malayopython*. Phylogeny after Reynolds et al. (2014) and Burbrink et al. (2020). Numbers at the nodes are the divergence times in Ma after Burbrink et al. (2020).

are closely associated to an underlying surface of osseous plates, but these scales are minute (Chen et al. 2011), and it is unclear if individualized elements can be recognized across specimens or species.

We identified a more satisfactory analogue in a different anatomical region. There is great diversity in the pholidotic patterns of the head in squamates, including mosaics of scales of a wide range of sizes, from proper scutes to small “granular” scales. In squamates excluding gekkotans and dibamids, scutes are fairly common in the “pileus region”: the dorsal surface of the head extending from the tip of the rostrum to the occiput. Notably, when scutes are found in the pileus, they have a tendency to be form similar arrangements, and individual scutes can be recognized between species (Ursel 1978; Estes et al. 1988) (Fig. 5).

In a manner roughly analogous to the mesochelydian plan, a stereotypical pileus scute pattern has been considered ancestral for squamates (Cope 1898; Ursel 1978; Estes et al. 1988), but different clades may have slight

variations of the ancestral pattern, and the homologies and evolution of the pileus scutes across squamate clades have not been comprehensively examined in a modern phylogenetic framework (Gauthier et al. 2008). Similar patterns of homologous cranial scutes are found in turtles, but this character complex remains even more understudied in the majority of turtle clades. Head scutation is used for the identification of marine turtles (Wyneken 2001), and has also been described for a limited number of stem turtles (Simpson 1938; Sterli and de la Fuente 2013; Evers et al. 2021).

Based on photographic data collected for a previous study (Esquerré and Keogh 2016), we hypothesize the loss and re-evolution of a typical pileus scute pattern within snakes. Boas and pythons (Boidae and Pythonidae, or Booidea and Pythonoidea of some authors), are two closely related clades, the Constrictores (Reynolds et al. 2014; Burbrink et al. 2020; Georgalis and Smith 2020). Species in these clades display pileus scale patterns ranging the scutes that are typical in most snakes

to granular scales with little differentiation. The latter condition is found in the majority of boa species. Early studies alternatively suggested that granular scales in the pileus represent the plesiomorphic (Zacharias 1898) or the derived (Werner 1899) condition for these clades. The modern phylogenetic understanding of snake phylogeny (Reynolds et al. 2014; Burbrink et al. 2020) suggests that medium-sized scales or large scutes in the typical snake pattern are likely primitive for both boas and pythons, but the typical scute pattern is also found deeply nested within boas, indicating its secondary acquisition (Fig. 5).

The head is a complex anatomical structure that tightly accommodates and supports diverse sense organs and mechanical feeding specializations, among other functions. Turtle shells, in contrast, provide a vessel for a large body cavity where organs are arranged more freely, and are routinely displaced due to head and limb tucking, food intake, and gravity. Unlike bones, most specific scales are not intimately associated with other critical components of the head (except the interoccipital scale with the pineal eye in lizards, and scales surrounding eyes and nares), and therefore the topography of the scutes should be more prone to vary with respect to the geometric and mechanical diversity of the vertebrate head. A worthy avenue of research would be to examine if the evolution of pholidotic patterns and scale size reflect the parallel ecological adaptations seen in the gross head geometry of pythons and boas (Esquerré and Keogh 2016). Ursel (1978) hypothesized that small scale size in the pileus facilitates increased cranial kinesis.

We infer that the scale systems of the turtle carapace and the pileus of squamates are subject to similar kinds of developmental biases (Uller et al. 2018), that strongly favour a narrow range of pholidotic arrangements when the scales are large and few. These biases are likely related to the intrinsic properties of the postulated reaction-diffusion processes that are involved in the patterning of skin appendages of the turtle carapace (Moustakas-Verho et al. 2014) and the body of amniotes in general, with some evidence of also being in place in the squamate head in particular (Milinkovitch et al. 2013), and indeed in the repeated skin appendages of vertebrates in general (Dhouailly et al. 2019). If this is correct, we postulate a highly conserved “pre-pattern” of scale placodes on the head of squamate embryos, and a highly conserved general system of periodic patterning. The latter is expected if evolution has difficulty traversing between distant parameter regions that yield viable Turing patterns (Scholes et al. 2019).

In turtles, a release from the bias towards the mesochelydian plan occurs in trionychians and *Dermochelys*, where the lack of scutes obviates the need for preserving a patterning morphogenetic process (Moustakas-Verho et al. 2014) (see above). However, carapacial scutes never significantly increase in number and reduce in size as the head scales of squamates do. It can be assumed that the pholidosis of the turtle carapace derives from a more traditional reptile pattern with numerous small scaled covering the trunk of the body, and for some unknown

mechanism caused the canalization of the patterns of basal testudinatans (canalization occurred again, to a lesser degree, with the origin of the Mesochelydia). We found in simulations with the reaction-diffusion model that by reducing diffusion rates, we can induce far greater numbers of scutes than in existent testudinatans, with a limit (Fig. 3B). Of course, in these simple experiments with an idealized model we are free to adjust parameters in ways that are not necessarily accessible to evolution due to physical limits and interactions with other developmental systems.

Unfortunately, the fossil record is unlikely to shed light in the matter. Unlike the bony shell (Li et al. 2008, 2018; Lyson et al. 2013; Schoch and Sues 2015), the early stages of the evolution of the shell scutes have not been documented in the fossil record in non-testudinatan stem turtles. For the sulci to form it is necessary a very close interaction between the epidermis and the bone surface, which likely did not occur in the earlier ancestors of turtles.

Conclusions

Developmental models aid palaeontologists to assess problems about character change in explicit causal frameworks. Even if the models do not suffice to explain all the relevant variation, they can shed light on matters previously only understood as far as the traditional approach of pattern-matching can reveal. In the carapace, the recent discoveries highlight the relationship between body segmentation and scute patterning, and how the same structures in the flanks of the carapace, –the carapacial ridges–, contribute to the formation of the outer ring of the carapace while possibly inducing its internal integumental patterning, as suggested by the temporal and causal priority of the marginals over the pleurals and vertebrals. We showed how the origin of the mesochelydian plan can be understood in these terms.

For the vast majority of turtles that retain their scutes, the macroevolutionary patterns are more complex and subtle than what might be conveyed by the “trend toward scute loss” that is traditionally suggested in the literature. Still, the reasons why scute number evolution remains highly constrained remain unknown, especially in contrast with what it is possible to induce in the developmental models, and also with what is seen in the diversity resulting from a similar developmental system in squamates.

On a more general note, we hope that this paper is an example of how considerations of ontogeny offer a deeper and necessary understanding of morphological transformations that occur in macroevolutionary time (Maier 2021). Our understanding of turtle evolution has benefited by work inspired by Wolfgang Maier, as in fundamental considerations of cranial anatomy (Werneburg and Maier 2019) or the evolution of the pleurodire shell (Scheyer et al. 2008).

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References

- Alibardi L (2003) Adaptation to the land: The skin of reptiles in comparison to that of amphibians and endotherm amniotes. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 298B: 12–41. <https://doi.org/10.1002/jez.b.24>
- Alibardi L, Dipietrangelo L (2005) Differentiation of the epidermis of scutes in embryos and juveniles of the tortoise *Testudo hermanni* with emphasis on beta-keratinization. *Acta Zoologica* 86: 205–216. <https://doi.org/10.1111/j.1463-6395.2005.00203.x>
- Anquetin J, Joyce WG (2014) A reassessment of the Late Jurassic turtle *Eurysternum wagleri* (Eucryptodira, Eurysternidae). *Journal of Vertebrate Paleontology* 34: 1317–1328. <https://doi.org/10.1080/02724634.2014.880449>
- Ascarrunz E, Sánchez-Villagra MR, Betancur-R R, Laurin M (2019) On trends and patterns in macroevolution: Williston's law and the branchiostegal series of extant and extinct osteichthyans. *BMC Evolutionary Biology* 19: 117. <https://doi.org/10.1186/s12862-019-1436-x>
- Biggs LC, Mikkola ML (2014) Early inductive events in ectodermal appendage morphogenesis. *Seminars in Cell & Developmental Biology* 25–26: 11–21. <https://doi.org/10.1016/j.semcdb.2014.01.007>
- Beggs K, Young J, Georges A, West P (2000) Ageing the eggs and embryos of the pig-nosed turtle, *Carettochelys insculpta* (Chelonia: Carettochelyidae), from northern Australia. *Canadian Journal of Zoology* 78: 373–392. <https://doi.org/10.1139/z99-214>
- Bentley BP, McGlashan JK, Bresette MJ, Wyneken J (2021) No evidence of selection against anomalous scute arrangements between juvenile and adult sea turtles in Florida. *Journal of Morphology* 282: 173–184. <https://doi.org/10.1002/jmor.21294>
- Benton MJ, Forth J, Langer MC (2014) Models for the rise of the dinosaurs. *Current Biology* 24: R87–R95. <https://doi.org/10.1016/j.cub.2013.11.063>
- Brophy TR, Ernst CH (2004) Sexual dimorphism, allometry and vertebral scute morphology in *Notochelys platynota* (Gray, 1834). *Hamadryad* 29: 80–88.
- Bujes CS, Verrastro L (2007) Supernumerary epidermal shields and carapace variation in Orbigny's slider turtles, *Trachemys dorbignii* (Testudines, Emydidae). *Revista Brasileira de Zoologia* 24: 666–672. <https://doi.org/10.1590/S0101-81752007000300018>
- Burbrink FT, Grazziotin FG, Pyron RA, Cundall D, Donnellan S, Irish F, Keogh JS, Kraus F, Murphy RW, Noonan B, Raxworthy CJ, Ruane S, Lemmon AR, Lemmon EM, Zaher H (2020) Interrogating genomic-scale data for Squamata (Lizards, Snakes, and Amphisbaenians) shows no support for key traditional morphological relationships. *Systematic Biology* 69: 502–520. <https://doi.org/10.1093/sysbio/sy062>
- Burke AC (1989) Development of the turtle carapace: Implications for the evolution of a novel bauplan. *Journal of Morphology* 199: 363–378. <https://doi.org/10.1002/jmor.1051990310>
- Campbell JA, Frost DR (1993) Anguid lizards of the genus *Abronia*: revisionary notes, descriptions of four new species, a phylogenetic analysis, and key. *Bulletin of the AMNH*. Available from: <http://digitallibrary.amnh.org/handle/2246/823> (February 27, 2020).
- Chen IH, Kiang JH, Correa V, Lopez MI, Chen P-Y, McKittrick J, Meyers MA (2011) Armadillo armor: mechanical testing and micro-structural evaluation. *Journal of the Mechanical Behavior of Biomedical Materials* 4: 713–722. <https://doi.org/10.1016/j.jmbbm.2010.12.013>
- Cherepanov G (2019) Morphogenetic and constructional differences of the carapace of aquatic and terrestrial turtles and their evolutionary significance. *Journal of Morphology* 280: 1571–1581. <https://doi.org/10.1002/jmor.21050>
- Cherepanov GO (1992) New morphogenetic data on the turtle shell: discussion on the origin of the horny and bony parts. *Studia Geologica Salmanticensia. Studia Geologica Salmanticensia. Studia Palaeocheloniologica* 3: 9–24.
- Cherepanov GO (2006) Ontogenesis and evolution of horny parts of the turtle shell. In: Danilov IG, Parham JF (Eds), *Fossil turtle research. Russian Journal of Herpetology*. Saint Petersburg, Russia, 19–33.
- Cherepanov GO (2014) Patterns of scute development in turtle shell: Symmetry and asymmetry. *Paleontological Journal* 48: 1275–1283. <https://doi.org/10.1134/S0031030114120028>
- Cherepanov GO (2015) Scute's polymorphism as a source of evolutionary development of the turtle shell. *Paleontological Journal* 49: 1635–1644. <https://doi.org/10.1134/S003103011514004X>
- Cherepanov GO (2016) Nature of the turtle shell: morphogenetic causes of bone variability and its evolutionary implication. *Paleontological Journal* 50: 1641–1648. <http://dx.doi.org/10.1134/S0031030116140033>
- Cherepanov GO, Malashichev Y, Danilov I (2019) Supernumerary scutes verify a segment-dependent model of the horny shell development in turtles. *Journal of Anatomy* 235: 836–846. <https://doi.org/10.1111/joa.13022>
- Clarac F, Scheyer TM, Desojo JB, Cerda IA, 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. <https://doi.org/10.1098/rstb.2019.0132>
- Cope ED (1886) An analytical table of the genera of snakes. *Proceedings of the American Philosophical Society* 23: 479–499.
- Cope ED (1898) The crocodilians, lizards, and snakes of North America. In: *Report of the United States National Museum for the year ending June 30, 1898*. Government Printing Office, Washington DC, United States, 153–270. Available from: <http://repository.si.edu/xmlui/handle/10088/29934> (August 21, 2021).
- Cordero GA (2021) Disentangling the correlated evolution of body size, life history, and ontogeny in miniaturized chelydroid turtles. *Evolution & Development* 23: 439–458. <https://doi.org/10.1111/ede.12386>
- Cordero GA, Vlachos E (2021) Reduction, reorganization and stasis in the evolution of turtle shell elements. *Biological Journal of the Linnean Society*. <https://doi.org/10.1093/biolinnean/blab122>

- Danilov IG (2005) Die fossilen Schildkröten Europas. In: Fritz U (Ed.), Handbuch der Reptilien und Amphibien Europas. Band 3/IIIB: Schildkröten (Testudines) II (Cheloniidae, Dermochelyidae, Fossile Schildkröten Europas). AULA-Verlag, Wiebelsheim, Germany, 329–441.
- Davenport J, Plot V, Georges J-Y, Doyle TK, James MC (2011) Pleated turtle escapes the box – shape changes in *Dermochelys coriacea*. Journal of Experimental Biology 214: 3474–3479. <https://doi.org/10.1242/jeb.057182>
- Delfino M, Scheyer TM, Fritz U, Sánchez-Villagra MR (2010) An integrative approach to examining a homology question: shell structures in soft-shell turtles. Biological Journal of the Linnean Society 99: 462–476. <https://doi.org/10.1111/j.1095-8312.2009.01356.x>
- Di-Poi N, Milinkovitch MC (2016) The anatomical placode in reptile scale morphogenesis indicates shared ancestry among skin appendages in amniotes. Science Advances 2: e1600708. <https://doi.org/10.1126/sciadv.1600708>
- Dhouailly D, Godefroit P, Martin T, Nonchev S, Caraguel F, Oftedal O (2019) Getting to the root of scales, feather and hair: As deep as odontodes? Experimental Dermatology 28: 503–508. <https://doi.org/10.1111/exd.13391>
- Dunson WA (1986) Estuarine Populations of the snapping turtle (*Chelydra*) as a model for the evolution of marine adaptations in reptiles. Copeia 1986: 741–756. <https://doi.org/10.2307/1444958>
- Erwin DH (2007) Disparity: morphological pattern and developmental context. Palaeontology 50: 57–73. <https://doi.org/10.1111/j.1475-4983.2006.00614.x>
- Escalona T, Weadick CJ, Antunes A (2017) Adaptive patterns of mitogenome evolution are associated with the loss of shell scutes in turtles. Molecular Biology and Evolution 34: 2522–2536. <https://doi.org/10.1093/molbev/msx167>
- Esquerré D, Keogh JS (2016) Parallel selective pressures drive convergent diversification of phenotypes in pythons and boas. Ecology Letters 19: 800–809. <https://doi.org/10.1111/ele.12620>
- Estes R, de Queiroz K, Gauthier J (1988) Phylogenetic relationships within Squamata. In: Estes R, Pregill G (Eds), Phylogenetic relationships of the lizard families. Stanford University Press, Stanford, California, United States, 119–281.
- Evers SW, Benson RBJ (2019) A new phylogenetic hypothesis of turtles with implications for the timing and number of evolutionary transitions to marine lifestyles in the group. Palaeontology 62: 93–134. <https://doi.org/10.1111/pala.12384>
- Evers SW, Barrett PM, Benson RBJ (2019a) Anatomy of Rhinohelys pulchiceps (Protostegidae) and marine adaptation during the early evolution of chelonoids. PeerJ 7: e6811. <https://doi.org/10.7717/peerj.6811>
- Evers SW, Neenan JM, Ferreira GS, Werneburg I, Barrett PM, Benson RBJ (2019b) Neurovascular anatomy of the protostegid turtle Rhinohelys pulchiceps and comparisons of membranous and endosseous labyrinth shape in an extant turtle. Zoological Journal of the Linnean Society: zlz063. <https://doi.org/10.1093/zoolinnean/zzz063>
- Evers SW, Rollot Y, Joyce WG (2021) New interpretation of the cranial osteology of the Early Cretaceous turtle *Arundelemys dardeni* (Paracryptodira) based on a CT-based re-evaluation of the holotype. PeerJ 9: e11495. <https://doi.org/10.7717/peerj.11495>
- Flatt T (2005) The evolutionary genetics of canalization. The Quarterly Review of Biology 80: 287–316. <https://doi.org/10.1086/432265>
- Fofonjka A, Milinkovitch MC (2021) Reaction-diffusion in a growing 3D domain of skin scales generates a discrete cellular automaton. Nature Communications 12: 2433. <https://doi.org/10.1038/s41467-021-22525-1>
- Fossette S, Gleiss AC, Myers AE, Garner S, Liebsch N, Whitney NM, Hays GC, Wilson RP, Lutcavage ME (2010) Behaviour and buoyancy regulation in the deepest-diving reptile: the leatherback turtle. Journal of Experimental Biology 213: 4074–4083. <https://doi.org/10.1242/jeb.048207>
- Gadow H (1899) Orthogenetic variation in the shells of Chelonia. Arthur Willey's Zoological Results, part 3: 207–222.
- Gaffney ES (1972) The systematics of the North American family Baenidae (Reptilia, Cryptodira). Bulletin of the AMNH ; v. 147, article 5. Available from: <https://digitallibrary.amnh.org/handle/2246/1098> (May 26, 2021).
- Gaffney ES (1990) The comparative osteology of the Triassic turtle *Proganochelys*. Bulletin of the American Museum of Natural History 194: 1–263.
- Gaffney ES, Hutchison JH, Jenkins FA, Meeker LJ (1987) Modern turtle origins: the oldest known cryptodire. Science 237: 289–291. <https://doi.org/10.1126/science.237.4812.289>
- Gauthier J, Kearney M, Bezy RL (2008) Homology of cephalic scales in xantusiid lizards, with comments on night lizard phylogeny and morphological evolution. Journal of Herpetology 42: 708. <https://doi.org/10.1670/07-047R2.1>
- Georgalis GL, Joyce WG (2017) A review of the fossil record of Old World turtles of the clade *Pan-Trionychidae*. Bulletin of the Peabody Museum of Natural History 58: 115–208. <https://doi.org/10.3374/014.058.0106>
- Georgalis GL, Smith KT (2020) Constrictores Oppel, 1811 – the available name for the taxonomic group uniting boas and pythons. Vertebrate Zoology 70: 291–304. <https://doi.org/10.26049/VZ70-3-2020-03>
- Gierer A, Meinhardt H (1972) A theory of biological pattern formation. Kybernetik 12: 30–39. <https://doi.org/10.1007/BF00289234>
- Gilbert SF, Loredó GA, Brukman A, Burke AC (2001) Morphogenesis of the turtle shell: the development of a novel structure in tetrapod evolution. Evolution & development 3: 47–58.
- Girgis S (1961) Aquatic respiration in the common Nile turtle *Trionyx triunguis* (Forskål). Comparative Biochemistry and Physiology 3: 206–217. [https://doi.org/10.1016/0010-406X\(61\)90056-1](https://doi.org/10.1016/0010-406X(61)90056-1)
- Guerrero A, Pérez-García A (2021) Morphological variability and shell characterization of the European uppermost Jurassic to lowermost Cretaceous stem turtle *Pleurosternon bullockii* (Paracryptodira, Pleurosternidae). Cretaceous Research 125: 104872. <https://doi.org/10.1016/j.cretres.2021.104872>
- Harmon LJ (2018) Phylogenetic comparative methods: learning from trees. Available from: <https://lukejharmon.github.io/pcm> (May 22, 2018).
- Harvey MG, Rabosky DL (2018) Continuous traits and speciation rates: alternatives to state-dependent diversification models. Methods in Ecology and Evolution 9: 984–993. <https://doi.org/10.1111/2041-210X.12949>
- Herrera-Alsina L, van Els P, Etienne RS (2019) Detecting the dependence of diversification on multiple traits from phylogenetic trees and trait data. Systematic Biology 68: 317–328. <https://doi.org/10.1093/sysbio/syy057>
- Hirayama R (1997) Distribution and diversity of Cretaceous chelonoids. In: Callaway J, Nicholls EL (Eds), Ancient marine reptiles. Academic Press, 225–241.
- Hirayama R, Chitoku T (1996) 1022 Family Dermochelyidae (superfamily Chelonioidea) from the Upper Cretaceous of North Japan. In: Transactions and proceedings of the Paleontological Society of Japan. New series. Paleontological Society of Japan, 597–622.

- Horváth E, Danko S, Havaš P, Schindler M, Šebela M, Halpern B, Csibrányi B, Farkas B, Kaňuch P, Uhrin M (2021) Variation in shell morphology of the European pond turtle, *Emys orbicularis*, in fragmented central European populations. *Biological Journal of the Linnean Society* 132: 134–147. <https://doi.org/10.1093/biolinnean/blaa184>
- Hunt G (2006) Fitting and comparing models of phyletic evolution: random walks and beyond. *Paleobiology* 32: 578–601. <https://doi.org/10.1666/05070.1>
- Jablonski D (2008) Species selection: theory and data. *Annual Review of Ecology, Evolution, and Systematics* 39: 501–524. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173510>
- Joyce WG (2014) A review of the fossil record of turtles of the clade *Pan-Carettochelys*. *Bulletin of the Peabody Museum of Natural History* 55: 3–33.
- Joyce WG (2016) A review of the fossil record of turtles of the clade *Pan-Chelydridae*. *Bulletin of the Peabody Museum of Natural History* 57: 21–56.
- Joyce WG (2017) A review of the fossil record of basal Mesozoic Turtles. *Bulletin of the Peabody Museum of Natural History* 58: 65–113. <https://doi.org/10.3374/014.058.0105>
- Joyce WG, Bell CJ (2004) A review of the comparative morphology of extant testudinoid turtles (Reptilia: Testudines). *Asiatic Herpetological Research* 10: 53–109.
- Joyce WG, Lucas SG, Scheyer TM, Heckert AB, Hunt AP (2009) A thin-shelled reptile from the Late Triassic of North America and the origin of the turtle shell. *Proceedings of the Royal Society B: Biological Sciences* 276: 507–513. <https://doi.org/10.1098/rspb.2008.1196>
- Joyce WG, Lyson TR (2015) A Review of the fossil record of turtles of the clade Baenidae. *Bulletin of the Peabody Museum of Natural History* 56: 147–183. <https://doi.org/10.3374/014.056.0203>
- Joyce WG, Bourque JR (2016) A review of the fossil record of turtles of the clade Pan-Kinosternoidea. *Bulletin of the Peabody Museum of Natural History* 57: 57–95.
- Joyce WG, Mäuser M (2020) New material of named fossil turtles from the Late Jurassic (late Kimmeridgian) of Wattendorf, Germany. *PLOS ONE* 15: e0233483. <https://doi.org/10.1371/journal.pone.0233483>
- Joyce WG, Sterli J, Chapman SD (2014) The skeletal morphology of the solemydid turtle *Naomichelys speciosa* from the Early Cretaceous of Texas. *Journal of Paleontology* 88: 1257–1287. <https://doi.org/10.1666/14-002>
- Joyce WG, Micklich N, Schaal SFK, Scheyer TM (2012) Caught in the act: the first record of copulating fossil vertebrates. *Biology Letters* 8: 846–848. <https://doi.org/10.1098/rsbl.2012.0361>
- Kordikova EG (2002) Heterochrony in the evolution of the shell of Chelonia. Part 1: Terminology, Cheloniidae, Dermochelyidae, Trionychidae, Cyclanorbidae and Carettochelyidae. *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen*: 343–417. <https://doi.org/10.1127/njgpa/226/2002/343>
- Li C, Fraser NC, Rieppel O, Wu X-C (2018) A Triassic stem turtle with an edentulous beak. *Nature* 560: 476–479. <https://doi.org/10.1038/s41586-018-0419-1>
- Li C, Wu X-C, Rieppel O, Wang L-T, Zhao L-J (2008) An ancestral turtle from the Late Triassic of southwestern China. *Nature* 456: 497–501. <https://doi.org/10.1038/nature07533>
- Lichtig AJ, Lucas SG (2021) *Chinlechelys* from the Upper Triassic of New Mexico, USA, and the origin of turtles. *Palaeontologia Electronica* 24: a13. <https://doi.org/10.26879/886>
- Lively JR (2016) Baenid turtles of the Kaiparowits Formation (Upper Cretaceous: Campanian) of southern Utah, USA. *Journal of Systematic Palaeontology* 14: 891–918. <https://doi.org/10.1080/14772019.2015.1120788>
- Lyson TR, Bever GS, Scheyer TM, Hsiang AY, Gauthier JA (2013) Evolutionary origin of the turtle shell. *Current Biology* 23: 1113–1119. <https://doi.org/10.1016/j.cub.2013.05.003>
- Maddison WP, Midford PE, Otto SP (2007) Estimating a binary character's effect on speciation and extinction. *Systematic Biology* 56: 701–710. <https://doi.org/10.1080/10635150701607033>
- Maffucci F, Pace A, Affuso A, Ciampa M, Treglia G, Pignalosa A, Hochscheid S (2020) Carapace scute pattern anomalies in the loggerhead turtle: are they indicative of hatchling's survival probability? *Journal of Zoology* 310: 315–322. <https://doi.org/10.1111/jzo.12754>
- Maier W (2021) *Der Weg zum Menschen*. 2nd Edition. Scidinge Hall
- Milinkovitch MC, Manukyan L, Debry A, Di-Poï N, Martin S, Singh D, Lambert D, Zwicker M (2013) Crocodile head scales are not developmental units but emerge from physical cracking. *Science* 339: 78–81. <https://doi.org/10.1126/science.1226265>
- Moustakas-Verho JE, Cherepanov GO (2015) The integumental appendages of the turtle shell: An evo-devo perspective. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 324: 221–229. <https://doi.org/10.1002/jez.b.22619>
- Moustakas-Verho JE, Zimm R, Cebrá-Thomas J, Lempiäinen NK, Kallonen A, Mitchell KL, Hämäläinen K, Salazar-Ciudad I, Jernvall J, Gilbert SF (2014) The origin and loss of periodic patterning in the turtle shell. *Development* 141: 3033–3039. <https://doi.org/10.1242/dev.109041>
- Nagashima H, Kuraku S, Uchida K, Kawashima-Ohya Y, Narita Y, Kuratani S (2012) Body plan of turtles: an anatomical, developmental and evolutionary perspective. *Anatomical science international* 87: 1–13.
- Nagashima H, Shibata M, Taniguchi M, Ueno S, Kamezaki N, Sato N (2014) Comparative study of the shell development of hard- and soft-shelled turtles. *Journal of Anatomy* 225: 60–70. <https://doi.org/10.1111/joa.12189>
- Nakajima Y, Danilov IG, Hirayama R, Sonoda T, Scheyer TM (2017) Morphological and histological evidence for the oldest known soft-shell turtles from Japan. *Journal of Vertebrate Paleontology* 37: e1278606. <https://doi.org/10.1080/02724634.2017.1278606>
- Nakov T, Beaulieu JM, Alverson AJ (2019) Diatoms diversify and turn over faster in freshwater than marine environments. *Evolution* 73: 2497–2511. <https://doi.org/10.1111/evo.13832>
- Newman HH (1906) The significance of scute and plate “abnormalities” in Chelonia: a contribution to the evolutionary history of the chelonian carapace and plastron. *The Biological Bulletin* 10: 68–107.
- Olivera-Martínez I, Viallet JP, Michon F, Pearton DJ, Dhouailly D (2004) The different steps of skin formation in vertebrates. *The International Journal of Developmental Biology* 48: 107–115. <https://doi.org/10.1387/ijdb.15272376>
- Pérez-García A, Codrea V (2018) New insights on the anatomy and systematics of *Kallokibotion* Nopcsa, 1923, the enigmatic uppermost Cretaceous basal turtle (stem Testudines) from Transylvania. *Zoological Journal of the Linnean Society* 182: 419–443. <https://doi.org/10.1093/zoolinnean/zlx037>
- Pimiento C, Tang KL, Zamora S, Klug C, Sánchez-Villagra MR (2018) Assessing canalisation of intraspecific variation on a macroevolutionary scale: the case of crinoid arms through the Phanerozoic. *PeerJ* 6: e4899. <https://doi.org/10.7717/peerj.4899>

- Pritchard PCH (1979) Encyclopedia of turtles. 1st ed. TFH New Jersey, United States.
- Procter JB (1922) A study of the remarkable tortoise, *Testudo loveridgii* Blgr., and the morphogeny of the chelonian carapace. Proceedings of the Zoological Society of London 92: 483–526. <https://doi.org/10.1111/j.1096-3642.1922.tb02155.x>
- Reynolds RG, Niemiller ML, Revell LJ (2014) Toward a tree-of-life for the boas and pythons: multilocus species-level phylogeny with unprecedented taxon sampling. Molecular Phylogenetics and Evolution 71: 201–213. <https://doi.org/10.1016/j.ympev.2013.11.011>
- Rice R, Riccio P, Gilbert SF, Cebra-Thomas J (2015) Emerging from the rib: resolving the turtle controversies. Journal of Experimental Zoology Part B: Molecular and Developmental Evolution 324: 208–220. <https://doi.org/10.1002/jez.b.22600>
- Rieppel O (2017) Turtles as hopeful monsters: origins and evolution. Indiana University Press, Bloomington, Indiana, United States, 208 pp.
- Rougier GW, de la Fuente MS, Arcucci AB (1995) Late Triassic turtles from South America. Science 268: 855–858.
- Sánchez-Villagra MR, Müller H, Sheil CA, Scheyer TM, Nagashima H, Kuratani S (2009) Skeletal development in the Chinese soft-shelled turtle *Pelodiscus sinensis* (Testudines: Trionychidae). Journal of Morphology 270: 1381–1399. <https://doi.org/10.1002/jmor.10766>
- Scheyer T, Martin Sander P, Joyce W, Bohme W, Witzel U (2007) A plywood structure in the shell of fossil and living soft-shelled turtles (Trionychidae) and its evolutionary implications. Organisms Diversity & Evolution 7: 136–144. <http://dx.doi.org/10.1016/j.ode.2006.03.002>
- Scheyer TM, Brüllmann B, Sánchez-Villagra MR (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. <https://doi.org/10.1002/jmor.10637>
- Scheyer TM, Werneburg I, Mitgutsch C, Delfino M, Sánchez-Villagra MR (2013) Three ways to tackle the turtle: integrating fossils, comparative embryology, and microanatomy. In: Brinkman DB, Holroyd PA, Gardner JD (Eds), Morphology and Evolution of Turtles. Vertebrate Paleobiology and Paleoanthropology. Springer Netherlands, Dordrecht, 63–70. https://doi.org/10.1007/978-94-007-4309-0_6
- Schoch RR, Sues H-D (2015) A Middle Triassic stem-turtle and the evolution of the turtle body plan. Nature 523: 584–587. <https://doi.org/10.1038/nature14472>
- Scholes NS, Schnoerr D, Isalan M, Stumpf MPH (2019) A Comprehensive network atlas reveals that Turing patterns are common but not robust. Cell Systems 9: 243–257.e4. <https://doi.org/10.1016/j.cels.2019.07.007>
- Simpson GG, Williams CS (1938) *Crossochelys*, Eocene horned turtle from Patagonia. Bulletin of the American Museum of Natural History 74: 221–254.
- Sterli J, Fuente MS de la (2013) New evidence from the Palaeocene of Patagonia (Argentina) on the evolution and palaeo-biogeography of Meiolaniformes (Testudinata, new taxon name). Journal of Systematic Palaeontology 11: 835–852. <https://doi.org/10.1080/14772019.2012.708674>
- Sterli J, Martínez RN, Cerda IA, Apaldetti C (2021) Appearances can be deceptive: bizarre shell microanatomy and histology in a new Triassic turtle (Testudinata) from Argentina at the dawn of turtles. Papers in Palaeontology 7: 1097–1132. <https://doi.org/10.1002/spp2.1334>
- Stone PA, Dobie JL, Henry RP (1992) Cutaneous surface area and bimodal respiration in soft-shelled (*Trionyx spiniferus*), stinkpot (*Sternotherus odoratus*), and mud turtles (*Kinosternon subrubrum*). Physiological Zoology 65: 311–330.
- Sullivan PM, Joyce WG (2017) The shell and pelvic anatomy of the Late Jurassic turtle *Platychelys oberndorferi* based on material from Solothurn, Switzerland. Swiss Journal of Palaeontology 136: 323–343. <https://doi.org/10.1007/s13358-017-0136-7>
- Szczygielski T, Sulej T (2016) Revision of the Triassic European turtles *Proterochersis* and *Murrhardtia* (Reptilia, Testudinata, Proterochersidae), with the description of new taxa from Poland and Germany. Zoological Journal of the Linnean Society 177: 395–427. <https://doi.org/10.1111/zoj.12374>
- Szczygielski T, Sulej T (2019) The early composition and evolution of the turtle shell (Reptilia, Testudinata). Benson R (Ed.). Palaeontology 62: 375–415. <https://doi.org/10.1111/pala.12403>
- Szczygielski T, Słowiak J, Drózd D (2018) Shell variability in the stem turtles *Proterochersis* spp. PeerJ 6: e6134. <https://doi.org/10.7717/peerj.6134>
- Thompson DW (1942) On growth and form. 2nd ed. Cambridge University Press, London.
- Thomson RC, Spinks PQ, Shaffer HB (2021) A global phylogeny of turtles reveals a burst of climate-associated diversification on continental margins. Proceedings of the National Academy of Sciences 118. <https://doi.org/10.1073/pnas.2012215118>
- Tong H, Brinkman D (2013) A new species of *Sinemys* (Testudines: Cryptodira: Sinemydidae) from the Early Cretaceous of Inner Mongolia, China. Palaeobiodiversity and Palaeoenvironments 93: 355–366.
- Turing AM (1952) The chemical basis of morphogenesis. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 237: 37–72.
- Turtle Taxonomy Working Group (2017) Turtles of the world: Annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status (8th Ed.). Chelonian Research Monographs 7: 1–292. <https://doi.org/10.3854/crm.7.checklist.atlas.v8.2017>
- Uller T, Moczek AP, Watson RA, Brakefield PM, Laland KN (2018) Developmental bias and evolution: a regulatory network perspective. Genetics 209: 949–966.
- Ultsch GR, Herbert CV, Jackson DC (1984) The comparative physiology of diving in North American freshwater turtles. I. Submergence tolerance, gas exchange, and acid-base balance. Physiological Zoology 57: 620–631.
- Ursel F (1978) Der Pileus der Squamata. Stuttgarter Beiträge zur Naturkunde 307. Available from: <https://www.biodiversitylibrary.org/page/33430927>.
- Waddington CH (1957) The strategy of the genes. Routledge, London, 274 pp.
- Wang B, Yang W, Sherman VR, Meyers MA (2016) Pangolin armor: overlapping, structure, and mechanical properties of the keratinous scales. Acta Biomaterialia 41: 60–74. <https://doi.org/10.1016/j.actbio.2016.05.028>
- Weinell J, Hooper E, Leviton A, Brown R (2019) Illustrated key to the snakes of the Philippines. Proceedings of the California Academy of Sciences 66: 1–49.
- Werneburg I, Maier W (2019) Diverging development of akinetic skulls in cryptodire and pleurodire turtles: an ontogenetic and phylogenetic study. Vertebrate Zoology 69 (2), 113–143.
- Werner F (1899) Phylogenetische Studien über die Homologien und Veränderungen der Kopfschilder bei den Schlangen. Arbeiten aus dem Zoologischen Institute der Universität Wien und der Zoologischen Station in Triest 11: 117–162.
- Yntema CL (1968) A series of stages in the embryonic development of *Chelydra serpentina*. Journal of Morphology 125: 219–251. <https://doi.org/10.1002/jmor.1051250207>

- Zacharias HCE (1898) Die Phylogenese der Kopfschilder bei den Boi-
den. 35 pp. Available from: <http://archive.org/details/biostor-181221>
(August 12, 2021).
- Zangerl R (1959) Rudimentäre Carapaxbeschuppung bei jungen Exem-
plaren von *Carettochelys* und ihre morphogenetische Bedeutung.
Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich: 10.
- Zangerl R (1960) 3 The vertebrate fauna of the Selma Formation of
Alabama. Part V. An advanced cheloniid sea turtle. Chicago Natural
History Museum, Chicago, Illinois, United States, 60 pp. Available
from: <https://www.biodiversitylibrary.org/item/25178>.
- Zangerl R (1969) The turtle shell. In: Gans C, Bellairs A d'Albini, Par-
sons TS (Eds), Biology of the Reptilia. Morphology A. Academic
Press, London and New York, 311–339.
- Zangerl R, Johnson RG (1957) The nature of shield abnormalities in
the turtle shell. [Chicago]: Chicago Natural History Museum, 36 pp.
Available from: <http://archive.org/details/natureofshieldab1029zang>
(July 1, 2021).
- Zimm R (2019) On the development of the turtle scute pattern and the
origins of its variation. PhD thesis. University of Helsinki Avail-
able from: <https://helda.helsinki.fi/handle/10138/299142> (May 21,
2021).
- Zimm R, Bentley BP, Wyneken J, Moustakas-Verho JE (2017) Envi-
ronmental causation of turtle scute anomalies in ovo and in silico.
Integrative and Comparative Biology 57: 1303–1311. <https://doi.org/10.1093/icb/ix066>

Supplementary material 1

Control files for simulations

Authors: Ascarrunz E, Sánchez-Villagra MR (2022)

Data type: .zip

Explanation note: Control files for simulations with the reaction-diffusion model.

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