

A plywood structure in the shell of fossil and living soft-shelled turtles (Trionychidae) and its evolutionary implications

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Abstract

The shell of soft-shelled turtles (Cryptodira: Trionychidae) can be characterised by a flexible bridge region, the loss of peripherals and a flattened carapace that is covered not with keratinous shields but with a leathery dermis. Here, we give a detailed description of the bone histology of this natural body armour that is unique not only among turtles but also among all known vertebrates. The flat bone elements have a sandwich-like morphology, with an internal and external compact bone layer framing inner cancellous bone. The external cortex is subdivided into two separate zones. The outer zone of the external cortex, which encompasses the ornamentation pattern typical for trionychid turtle shell bones, is comprised of lamellar bone. Similarly, the whole of the internal cortex is comprised of lamellar bone. The inner zone of the external cortex, however, consists of a highly ordered, plywood-like arrangement of structural collagen fibre bundles within the bone and skin of the shell. The orientation of the collagenous fibres also prescribes the orientation of the mineral phase of the bone, the hydroxyl-apatite crystallites. Strikingly, this peculiar fibre bundle arrangement strongly resembles artificial reinforced fibre-strengthened polymeric materials that combine superior mechanical strength with low weight. We hypothesise that the evolutionary success of soft-shelled turtles is tied to this plywood-like structure of the skin and bone. It may have been the key adaptation that allowed trionychids to greatly reduce and flatten their protective shell, resulting in decreased mineral needs for hard tissues, improved camouflage and hunting performance, biomechanical stability of the shell, as well as overall increased agility and short-term swimming boosts. Significantly, it also may have enabled more efficient cutaneous breathing while still retaining effective armour in both the fossil and Recent trionychid turtles.

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Introduction

Among animals, turtles are one of the best examples of how natural body parts are used as armour. The turtle shell is a composite structure consisting of a

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domed inner bony component similar to the human skull diploe (Bloom and Fawcett 1994), i.e. flat bone in which cancellous bone is framed by an overlying and underlying compact bone layer. An outer component comprising keratinous shields is generally thought to fulfil some kind of armour function (Zangerl 1969), where the shields provide strength to the shell by systematically covering the sutural boundaries between the bony elements. Compared to this, the shell of trionychid turtles seems more fragile because it is typically flattened and almost disk-like in appearance (Zangerl 1969). The overlapping keratinous shields are lost, so that the bony carapace and plastron are covered by the upper layer of the dermis and the thin, leathery epidermis only (Ernst and Barbour 1989; Cherepanov 1992). As in many other aquatic turtles, the bony shell is reduced so that the rib ends are not fully covered by dermal bone. However, unlike in any other turtle, the peripheral bony plates of most trionychids are completely lost. The free rib ends are covered only by a rubbery skin flap. The exception to the rule is *Lissemys punctata* (Trionychidae: Cyclanorbininae), which still retains small bone elements in the periphery of the soft dermal part of the shell. Even though the V-shaped bone elements in *L. punctata* strongly resemble peripherals of hard-shelled turtle genera, there is still discussion if they are truly homologous structures (see Meylan 1987). In trionychids, the surfaces of the bony elements usually possess a characteristic sculptured ornamentation pattern consisting of ridges, pits and knobs, which renders even small fragments easily recognisable in fossil deposits.

The histological study of bone tissue poses a unique opportunity to comprehend and reconstruct the nature and structure of tissues that are generally not preserved in fossils because, similar to other soft tissues of the vertebrate body, skin usually has no potential to fossilise. Therefore, the study of dermal bone offers a rare, if not the only, possibility to study structural aspects of the integument of fossil specimens.

Nineteenth century anatomists (Rathke 1848; Hoffmann 1878, 1890) were puzzled by their histological observations of the dermis (= corium, Lederhaut), the lower integumentary layer of trionychid turtles. The dermis possesses a unique soft-tissue collagen fibre arrangement characterised by alternately oriented fibre bundles. Schmidt (1921) was the first to describe in detail the integument of the soft-shelled turtle *L. punctata*, known at that time as *Emyda granosa*, and to provide biomechanical interpretations of the observed histological structures. However, all mentioned studies focussed only on the soft-tissue microstructure of the dermis, preventing the authors from realising that the fibrous arrangement is not restricted to the soft-tissue part of the shell. Herein, we confirm the presence of such a peculiar fiber pattern in the skin of all studied trionychid turtles, and extend the observation to

the bony elements of the shell. This makes the fibrous tissue in the trionychid shell bones one of the most striking features of vertebrate bone microstructure.

Detailed analysis of the structures of the bone and skin showed astounding resemblance to fibre-reinforced composites (Preston 1983), materials that combine the advantages of light-weight construction with superior mechanical strength. However, detailed biomechanical analysis is beyond the scope of the present paper; instead, we focus on description of the microstructure of the trionychid shell.

Material and methods

Material

The material used for this study included fossil and Recent specimens of Trionychidae, as well as several fossil and Recent representatives of outgroup taxa. From the Carettochelyidae clade, the sister taxon to Trionychidae (Meylan 1987; Joyce et al. 2004), four genera were sampled: *Allaeochelys*, *Anosteira*, *Carettochelys* and *Pseudanosteira*. See the Appendix for a list of all taxa studied.

Collection abbreviations: FM = Field Museum, Chicago, USA; HLMD = Hessisches Landesmuseum Darmstadt, Germany; IPB = Institut für Paläontologie, Bonn, Germany; MAGNT = Museum and Art Gallery of the Northern Territory, Darwin, Australia; MB = Museum für Naturkunde, Berlin, Germany; ROM = Royal Ontario Museum, Toronto, Canada; SMNS = Staatliches Museum für Naturkunde Stuttgart, Germany; TMP = Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; UCMP = University of California Museum of Palaeontology, Berkeley, USA; YPM = Yale Peabody Museum of Natural History, New Haven, USA; ZFMK = Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.

Methods

This study is part of ongoing research on the bone histology of the turtle shell, in which basal turtles, pleurodires and cryptodires (including tortoises, freshwater and marine turtles) are sampled. Several elements of fossil and living turtle shells were sampled, including neurals, costals, peripherals and elements of the plastron. Bones of the carapace and plastron of fossil and Recent specimens were sectioned using a diamond rock saw. Planes of sectioning varied between the different shell bone elements (neurals were cut perpendicular to their anteroposterior axis; costals were cut parallel and/or perpendicular to the incorporated ribs;

peripherals of the outgroup taxa (including the ‘peripheral bones’ of *L. punctata*) were cut perpendicular to the anteroposterior axis of the turtle shell; plastron elements were cut parallel and/or perpendicular to the anteroposterior axis of the turtle shell). Secondary and tertiary sets of thin sections included 90° sections and sections taken on a tangential plane to the primary plane of sectioning. All individual bony elements were processed into sections approximately 80 µm thin or less, using standard procedures for petrographic thin sectioning as described, for example, by Scheyer and Sander (2004). The bone microstructure (micro-scale) of the thin sections was then studied with a standard polarising microscope in order to understand the three-dimensional arrangement of the observed structures. Thin sections of fossil specimens have two important advantages over the thin sections made from Recent bone. First, fossil bone is generally easier to process into thin sections, because the mineral content is almost 100% instead of about 46% in Recent bone. Due to the high content of organic tissue, i.e. collagen, Recent bone is prone to shrink or expand if heat or water is applied while processing the sections. Second, again due to the higher mineral content of the fossil bone, the polarising abilities of the thin sections are superior, resulting in high-contrast microscopic images.

Where applicable, scanning electron microscope (SEM) photographs were made to elucidate the microstructure (micro- and nano-scale) characteristics of the collagenous fibre bundles of the bony elements. For this purpose, polished planar sections of trionychid shell elements were etched for 3–5 s with hydrochloric acid (10%). After the acid had been neutralised with distilled water, the sections were fixed, gold-coated and analysed under the SEM.

Results

The diploe-like structure, where compact bone layers frame internal cancellous bone, is recognised within all thin sections of the trionychid shell elements. Such a build of the flat-shell elements is a plesiomorphic trait for all turtles, including Upper Triassic *Proganochelys quenstedti* Baur (Scheyer, pers. obs.), the basal-most turtle known today. The external compact bone layer can be subdivided into two zones. The ornamentation pattern (OP) of the carapacial elements of the trionychid shell represents the outer, more dorsal zone. The inner, more ventral zone (external to the inner cancellous bone) comprises the plywood-like pattern (Humphrey and Delange 2004) described below. In the bone elements of the plastron, the plywood-like pattern lies dorsal to the OP, which is the outer, more ventral zone here. The well-ordered arrangement of structural fibres

preserved through the mineral phase of the bone is even visible macroscopically at the edge of shell elements as light and dark bands and decussating striations, respectively (Figs. 1 and 2). In dried specimens, it becomes apparent that the plywood-like pattern originates, as the fibres of the corium are incorporated into the bone matter, through a process known as metaplastic ossification (Haines and Mohuiddin 1968).

The OP (see Fig. 1) of the outer zone encompasses reticular raised ridges and knobs. In thin sections, it is apparent that lamellar bone tissue builds up the OP.

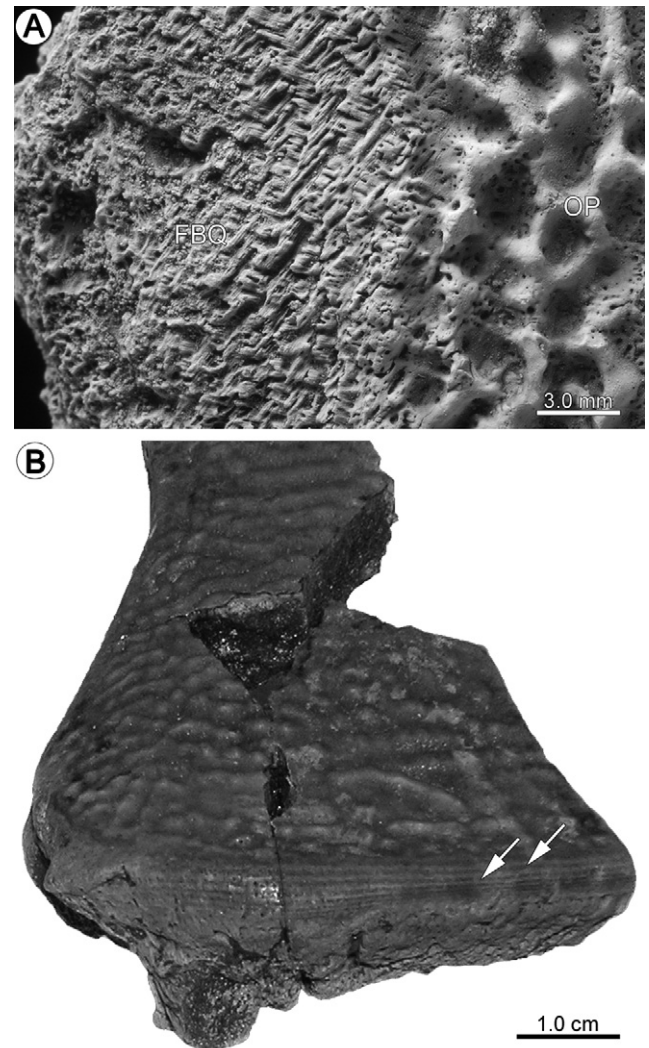


Fig. 1. Macroscopic evidence for the plywood-like structure within two elements of the trionychid turtle shell. (A) Detail of distal part of costal of fossil *Aspideretoides splendidus* (TMP 85.36.760); focus lies on margin of specimen, where FBQ seem to be etched out of the bone matrix; the decussating plies can be seen in spaces between the ornamentation; FBQ: collagen fibre bundles decussate, OP: trionychid ornamentation pattern. (B) Incomplete left hyoplastron of indeterminate fossil trionychid turtle (TMP 92.94.01); arrows: decussating structural collagen fibre plies shown as light and dark banding at margin.

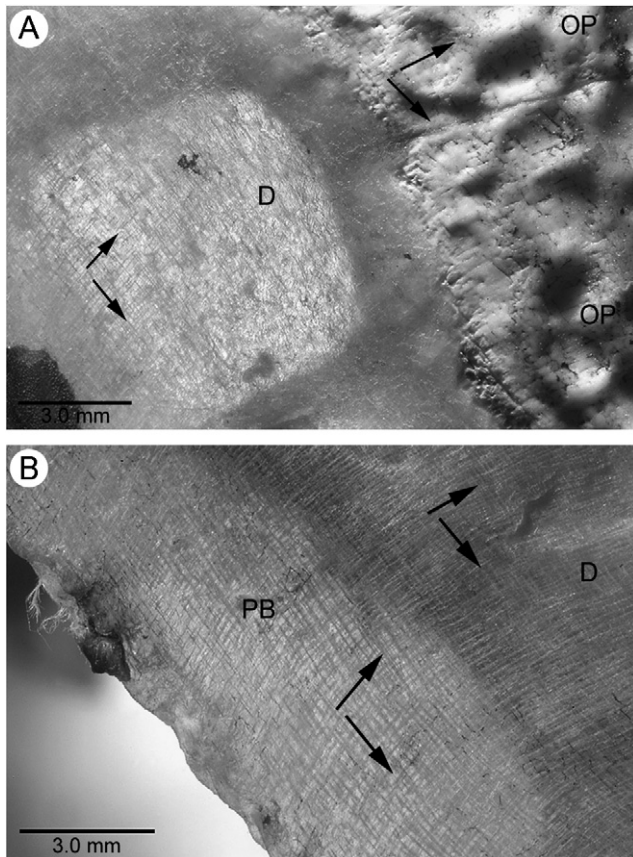


Fig. 2. (A) Detail of carapace of a dried juvenile *Trionyx triunguis* (IPB R 260); decussating fibre plies continue undisturbed from dermis into the bony margin of carapace; D: dermis, OP: reticular ornamentation patterns cover structural plies and FBQ of bony shell elements; arrows: FBQ decussate in carapacial skin. (B) Detail of plastron of same specimen; dermal tissue showing structural fibre plies is overlying a plastral bone; in later ontogenetic stages, plies/FBQ will be metaplastically incorporated into bone tissue as plastral parts continue to ossify; D: dermis, PB: plastral bone, arrows: FBQ decussate in plastral skin.

Sharpey's fibres (ShF) are observed to insert perpendicular to the surface of the bone in those ridges and knobs (Fig. 3, for colour version see the online edition), resulting in a fan-shaped pattern.

In the interior zones of the external cortex, we discerned up to ten distinct plywood-like layers (Fig. 3), with each ply being alternately rotated relative to those above and below (Figs. 3–5). In the studied fossil element of cf. *Aspideretoides* sp. (IPB R 533a; Fig. 3B), the angles in the ply-stack range about 45–50° relative to those above and below. However, angle values can be more variable in other trionychid genera. In the studied shell of *Trionyx triunguis* (IPB R260), the angles are generally wider and range between 70° and almost 90°.

Note that data in the following paragraph are based on the fossil specimen of cf. *Aspideretoides* sp. (IPB R 533a), due mainly to the reasons mentioned in the

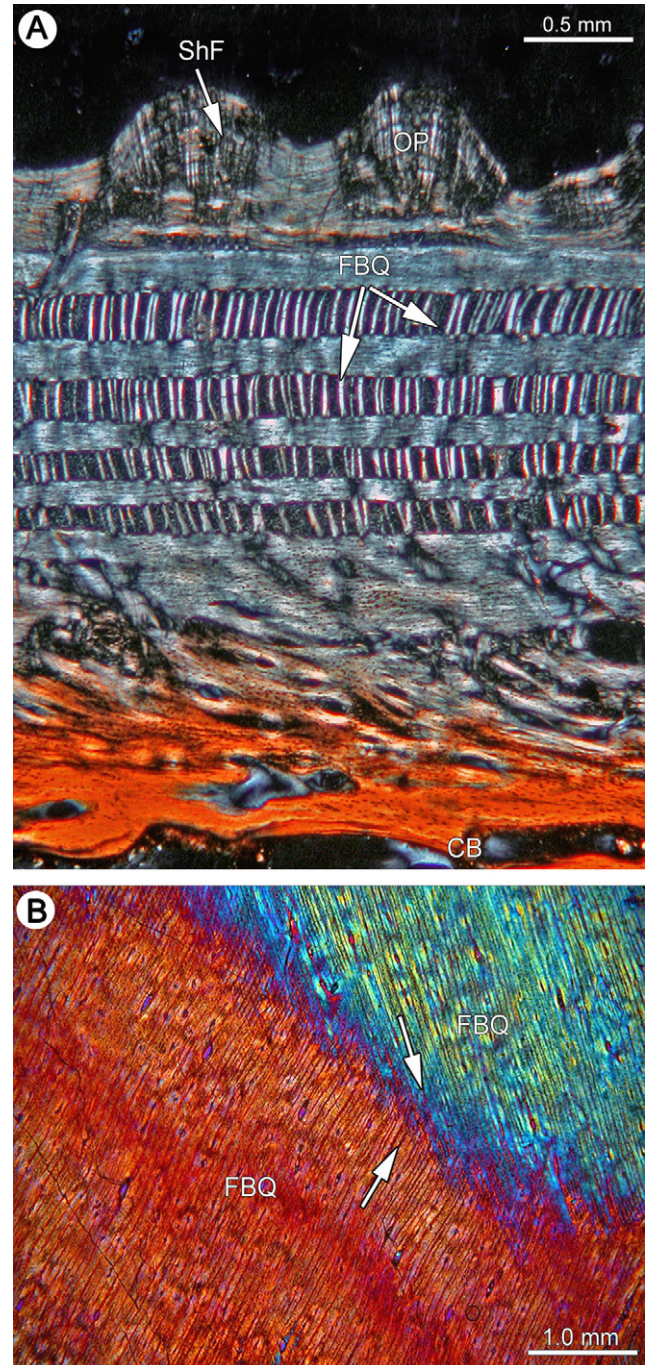


Fig. 3. (A) Thin section of costal fragment in cf. *Aspideretoides* sp. (IPB R 533a), focussing on external cortex; plane of sectioning perpendicular to long axis of rib and to surfaces of fragment; CB: cancellous bone; FBQ: black and white quadrangles between vertically oriented plies, OP: raised knob of ornamentation pattern, ShF: Sharpey's fibres. (B) Thin section of costal fragment of the same specimen (IPB R 533b), with plane of sectioning crossing tangentially through the external cortex at low angle (polarised light; gypsum red I); arrows: note decussating plies rotated about 45° to each other.

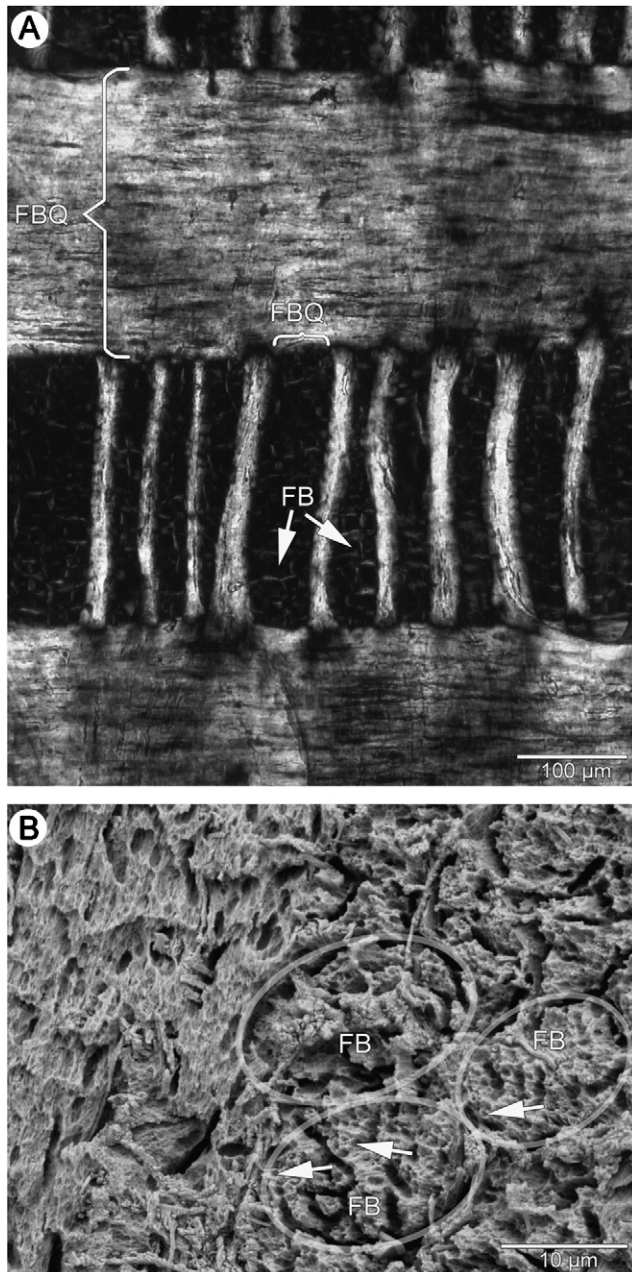


Fig. 4. (A) Close-up of plywood-like pattern of the inner zone of the external cortex in cf. *Aspideretoides* sp. (IPB R 533a); vertical fibre bundle quadrangles (FBQ) expand at bottom and at top to anchor to horizontal FBQ; single collagenous fibre bundles (FB) in dark horizontal FBQ are seen as black circles or polygons divided by thin white lines. (B) SEM image of inner zone of dorsal cortex in cf. *Aspideretoides* sp. (IPB R 533), focussing on the ply system; numerous etched surfaces of long axes of bone apatite crystallites (arrows) recognisable within horizontally trending FB (form enhanced by grey circles in three cases); orientation of apatite crystallites represents arrangement of single collagenous fibres within the FB.

Methods section (i.e. thin sections of fossil bones being of higher quality and naturally stained); angle values may well differ in other trionychid turtle taxa.

The plies of the second inner zone below the OP of the carapacial elements are composed of fibre bundle quadrangles (FBQ) that macroscopically appear in the skin as single fibre strands. At the top and bottom of each ply, some FBQ expand slightly to anchor the neighbouring bone layers (Fig. 4A). In polarised light of the fossilised bone, the plies are seen as dark and light bands and the FBQ as dark and light patches, respectively (Figs. 4,5). The long axes of the fibre bundles (FB) in each quadrangle are perpendicular to those in the neighbouring quadrangles. Those FBQ in which the FB trend horizontally usually contain up to three rows of FB, whereas the vertically pointing FBQ consist of two parallel FB rows. The FB can reach diameters of 10–20 μm and are composed of numerous single nano-scale collagen fibres (Fig. 4B). The layers of FBQ cross each other at approximately 45–55°, e.g. symmetrically to the long axes of costal plates and their incorporated ribs. The FBQ continue without interruption into the unossified part of the lower dermis. The plywood-like structure generally lies dorsal to the OP in the trionychid plastron. In the studied juvenile specimen of *Trionyx triunguis* (Fig. 2), however, the plastral bone is still without the OP. Here, the still unossified structural fibre plies covering the plastral bone are completely visible (Fig. 2B).

The cancellous bone of the shell elements is composed of a spongy meshwork of bone trabeculae. While the interstitial parts of the trabeculae retain some primary bone tissue, the remaining trabecular parts mainly show centripetally deposited lamellar bone tissue. In contrast to the complexity of the external cortex, the internal cortex is a single zone of lamellar bone. Within this zone, the bone lamellae can change angles, but it is not distinguishable if they follow a predominant direction in connection to the orientation of the shell element.

The sutures between the shell bones themselves, and the contacts between the bony elements of the shell and the leathery skin, represent potential zones of weakness. However, because the FBQ continue from the bony elements into the dermis (Fig. 3), the bones of the carapace and plastron are surrounded by a ring of toughened dermal tissue. Similarly, a bony bridge that would firmly connect the carapace with the plastron is absent in trionychid turtles. Instead, the two halves of the shell are held together by the fibre-reinforced skin, resulting in a flexible though tough bridge region.

Discussion

Although the cancellous bone and the internal cortex of the flat bones of the trionychid shell are rather similar to those recognised in other hard-shelled turtles, the plywood-like arrangement in the external cortex of the

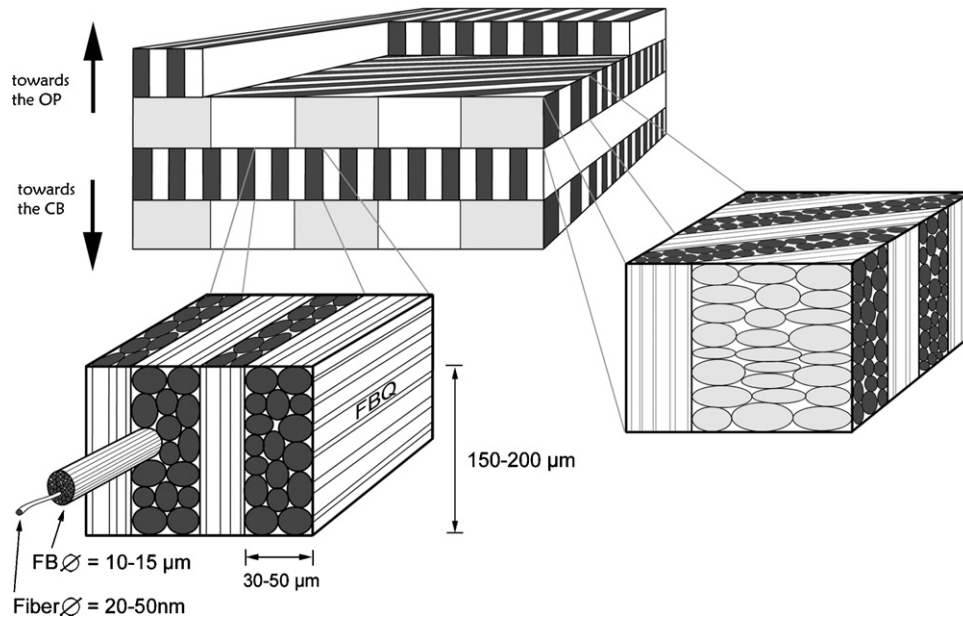


Fig. 5. Schematic of bone microstructure of dorsal cortex based on cf. *Aspideretoides* sp. (IPB R 533), illustrating the rotated ply system; actual microstructure, as seen in Fig. 4, is much more variable than implied here. Each ply consists of numerous fibre bundle quadrangles (FBQ) that consist of tubular fibre bundles (FB). Magnification of plywood-like structure highlights orientation of FBQ to each other, with neighbouring quadrangles rotated at 90° angles to each other. Each FB (10–15 µm) in the FBQ consists of multiple single collagen fibre strands (20–50 nm). Vertically trending FBQ that trend from ornamentation pattern towards cancellous bone are usually two FB rows thick, horizontal ones are usually three FB rows thick (30–50 µm). CB: cancellous bone, OP: ornamentation pattern.

bone is unique to the Trionychidae. Because this dermal structure of the shell bone and shell skin is found in all crown-group trionychid turtles, it can be considered a synapomorphy of this clade. However, due to the statistically small numbers of trionychid individuals studied and the resulting uncertainty concerning intraspecific variation, it remains unclear whether the measured angles between the ply stacks in the trionychid shell are characteristic at the genus- or even at the species level. Schmidt (1921) pointed out that the fibre bundles of the so called ‘Bündelschicht’ (plywood-like pattern) are arranged diagonally to the overall long axis of the turtle shell. He attributed this arrangement to a biomechanical retention of the shell curvature, or to resistance to the flattening of the shell. Structurally, the presence of Sharpey’s fibres in the outer zone, the OP, of the external cortex of the trionychid shell bones (Fig. 3) implies a strengthened anchoring of the integument onto the bone. The internal cortex and the inner cancellous bone of the bony shell elements are rather similar to those found in other hard-shelled turtles and are thus considered plesiomorphic.

At this point, a short comparison to Schmidt’s (1921) work seems to be in order, to elucidate similarities and discrepancies between his ‘soft-tissue’ analysis and our ‘hard-tissue’ analysis. All in all, the two works complement each other and lead to a clearer understanding of the trionychid turtle shell. Structures similar to those

presented herein were described in Schmidt’s interpretations and drawings of the soft-tissue part. We hypothesise that the tripartite organisation of the corium into an external ‘Bündelschicht’, an interior ‘Filzschicht’ and an internal ‘Grenzschicht’, as presented by Schmidt (1921, p. 195), corresponds to the metaplastically ossified bone of the trionychid shell with its ply system in the external cortex, the interior cancellous bone and the internal cortex. Even if, as Kälin (1945) pointed out, the initial ossification of the dermal bone begins below the ‘tiefes Stratum compactum’ (St. c.t.; Kälin 1945, p. 160; Fig. 11), which is synonymous to Schmidt’s ‘Grenzschicht’, the subsequent dermal ossification is strongly associated with the St. c.t., justifying our hypothesis of the equivalency of the tissues.

On the other hand, no deviating or anastomosing FBQ, as described by Schmidt, were recognised in the bone of the shell; thus, the FBQ appear to be less variable in the bony carapacial disk compared to the peripheral soft-tissue part of the shell. Furthermore, we do not follow Schmidt’s assertion that the vertical fibre bundles pervade continuously through the whole ply system. Though occasionally some vertical FBQ do seem to cross the horizontal plies, the majority of them appear to be discontinuous. As presented in Figs. 3 and 4, the vertical FBQ reach into the overlying and underlying plies and expand there to further anchor the ply system, but they do not continue on through the neighbouring plies.

Several specific adaptive advantages can be hypothesised for the flattening of the carapace, reduced ossification of the shell and the loss of the keratinous shields in the Trionychidae. First, trionychid turtles have selective advantages in building and maintaining less hard tissues, as the peripheral plates, distal parts of the costal plates and much of the plastral bones are reduced (e.g. Rathke 1848; Hoffman 1878; Zangerl 1969; Meylan 1987). The decreased demand for minerals and nutrients clearly represents a physiological advantage. Second, the reduced amount of hard tissues leads to an overall lower body mass, a point mentioned already by Schmidt (1921). The lower body mass facilitates at least fast short-term swimming and higher manoeuvrability, as is seen in many other secondarily aquatic tetrapods (Webb and Buffrénil 1990). The powerful swimming bursts (Pritchard 1984; Pace et al. 2001), which can be used either to quickly burrow into soft sediments for hiding (Pritchard 1984; Bramble, pers. comm., in Meylan 1987) or to escape from predators, are enabled through the flattened carapace with its movable soft-tissue peripheral flap together with the propelling front feet. Third, since trionychids are ambush predators that hide at the bottom of lakes and rivers, the flattened, easily buried carapace together with the snorkel-like nose increase their hiding abilities and hunting success. Fourth, a flattened shell that is covered with extremely slick and slippery skin is an effective protection against predators both in water and on land, because any predator will have difficulties grasping any flat object that tightly hugs the ground. In this instance, a long and agile neck and sharp beak not only is well suited for catching prey-like fishes (Pritchard 1984; see also discussion in Meylan 1987), but also makes a dangerous weapon that the trionychid turtle can use to effectively defend itself (authors' observation). Fifth, according to the striking parallels to man-made fibre-reinforced composite materials, the plywood-like structure may have some kind of biomechanical advantage, be it a heightened resistance against crushing or crack prevention, or simply an increase in stability of the flattened carapacial disk. Similar points were already listed by Schmidt (1921) for the soft-tissue part of the shell. These aspects of the plywood-like structure of trionychid shells require further biomechanical studies. Last but not least, the loss of keratinous shields allows for increased cutaneous breathing (Ultsch et al. 1984). Presumably, trionychid turtles are unique in their soft carapacial and plastral epidermis acting as an efficient cutaneous breathing organ, allowing a bimodal gas exchange with ambient water (Girgis 1961; Bagatto and Henry 1999). This additional method of respiration, together with buccopharyngeal breathing, allows soft-shelled turtles to remain submerged for a vastly increased period of time compared to turtles lacking this adaptation (Girgis 1961; Seymour 1982; Bagatto

and Henry 1999; Gordos et al. 2004). They seldom have to leave their hiding place or extend their long neck and snorkel-like nose to the surface to breathe, which again works in favour of camouflage. However, the reduction of the bony shell poses also a disadvantage by reducing the potential storage and buffering of lactic acid, lowering anoxic water tolerance (Jackson et al. 2000). Trionychid turtles prefer normoxic water habitats in which they can take full advantage of their ability to breathe through their expanded skin surface. Those normoxic habitats are also of great importance for hibernation, because trionychids cannot tolerate elevated levels of anoxia for longer periods of time (Reese et al. 2003).

Today, the two most prominent living turtle species, besides the Trionychidae with a leathery skin that covers the bony shell, are *Carettochelys insculpta* (sister taxon to the Trionychidae; see Meylan 1987) and *Dermochelys coriacea* (the marine leatherback turtle; see Zangerl 1969; Paladino et al. 1990). However, compared to trionychids these species do not show similar integumentary adaptations in their shell. Furthermore, no member of the studied fossil carettochelyid genera (*Allaeochelys*, *Anosteira*, and *Pseudanosteira*), fossil dermochelyid genera (*Psephophorus* and *Egyptemys*) and *Dermatemys mawii*, a Recent species with extremely thin keratinous shields, has developed structures similar to those found in the trionychid turtle shells. In this respect, it would also be interesting to investigate the shell composition of *Natator depressus*, a Recent cheloniid turtle taxon in which shields can also be reduced.

Measuring the evolutionary success of a group of organisms is difficult and may often seem speculative. Yet, trionychid turtles have experienced a certain evolutionary success, because the group originated more than 120 million years ago during the Early Cretaceous in Asia and eventually came to be one of the most cosmopolitan, long-lived turtle radiations by spreading to North America, Europe, Africa and Meganesia (e.g. Ernst and Barbour 1989; Iverson 1992). Since their first appearance in the fossil record, however, almost no variation has occurred in overall trionychid shell morphology, and fragments of their shells are among the most obvious and numerous fossil specimens in many Mesozoic or Cenozoic fossil lagerstätten. The current distribution of extant species appears to be limited only by access to suitable river habitat and temperature regions. We hypothesise that the trionychid shell with its unique composite structure evolved as an alternative lightweight solution to the plesiomorphic domed protection in other turtles, an adaptation that offers additional physiological and biomechanical advantages. However, it is uncertain if the highly unique morphology of trionychids originated and became fixed rapidly, because the record of pre-early Cretaceous fossil turtles still remains poorly documented and understood.

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Appendix. Turtle taxa and specimens studied

Fossil taxa are marked with a cross in parentheses.

Trionychidae: *Amyda cartilaginea*: ZFMK-14040; *Apalone ferox emoryi*: ZFMK-47482; *Apalone latus* (†): TMP 67.16.67; *Aspideretes gangeticus*: ZFMK-13563; *Aspideretoides splendidus* (†): TMP 85.36.760, TMP 89.116.61; *Aspideretoides* sp. (†): IPB R 533; *Cyclanorbis senegalensis*: ZFMK-83284; *Dogania subplana*: ZFMK-65847; *Lissemys punctata*: YPM 10882, YPM 11645, YPM 13153; *Palea steindachneri*: ZFMK-81541; *Pelodiscus sinensis*: ZFMK-58971; *Plastomenus* sp. (†): UCMP V81108/150227, UCMP V81110/150231; *Rafetus euphraticus*: ZFMK-13938; *Trionyx triunguis*: IPB R 260; *Trionyx* sp. (†): HLMD Me-8084, IPB HaH-3120, IPB HaH-3164; *Trionychidae* indet. (†): TMP 92.94.01, TMP 85.63.30.

Outgroup turtles: *Allaeochelys* sp. (†): HLMD-Me 10468; *Anosteira* sp. (†): FM PR 819; *Carettochelys insculpta*: MAGNT R12640; *Dermatemys mawii*: ZMB 9558; *Dermochelys coriacea*: YPM 10751; *Egyptemys eocaenus* (†): YPM 6212; *Emys orbicularis*: SMNS 6880; *Hesperotestudo crassiscutata* (†): ROM 51460, ROM 55400; *Psephophorus* sp. (†): MB. R. 2532.1; *Pseudanosteira* sp. (†): UCMP V85013/131731; *Testudo* sp.: SMNS 6820; *Trachemys scripta* (†): ROM 33693, ROM 33978, ROM 34287, ROM 34289.

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