

THE ORIGIN OF THE BONY SHELL OF TURTLES AS A UNIQUE EVOLUTIONARY MODEL IN REPTILES

Gennady O. Cherepanov¹

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Generally, the bony armor of reptiles consists of separate osteoderms which develop in the dermis independently from the internal skeleton. Such a dermal armor is characteristic of ancient pareiasaurs that are closely related to Testudines. On the basis of this fact it has been assumed that the turtle shell is built up as the fusion of the osteoderms with some elements of the internal skeleton. However, this concept is not confirmed by morphogenetic data. During turtle ontogeny the reduction of the trunk myomeres leads to sinking of the vertebrae and ribs into the dermis. The neural and costal plates of the dorsal disk form as the outgrowths of these endoskeletal bones on inside the dermis. There are no independent superficial ossicles over the general plastral bony primordia in the ventral region of the body. Each plastral plate develops only from a single primordium like the clavicles, interclavicle and gastralia of other reptiles. Most likely, Testudines progressed in a unique evolutionary direction. Their bony shell is mainly the result of modification and consolidation of internal skeletal elements. The real osteoderms develop only on the body margins as connections between the dorsal and the ventral discs.

Key words: Morphogeny, evolution, Testudinata.

The bony shell of turtles is a unique armored complex distinguishing these animals from all other reptiles. Phylogenetically, the shell is a very ancient structure: the oldest known *Proganochelys* already had a well-developed shell that differed little from that modern species. As a result of the huge morphological gap between Testudines and the other amniotes and the poorly documented fossil records of the earliest period of their evolution the problem of the origin of turtles and formation of their shell is very difficult. It is not by accident that more than ten different groups of early tetrapods have been identified as possible ancestors of turtles (see reviews by Romer, 1968; Laurin and Peisz, 1995). Now the concept that the turtle shell is built up by the fusion of the primary osteoderms with the elements of the internal skeleton is broadly accepted (Zangerl, 1969; Walker, 1973; Meylan, 1987; Laurin and Peisz, 1995; Lee, 1995, 1996; etc.) However, this view is based only on indirect data and disputable arguments. The present paper is an attempt to call attention to some new information concerning the morphogenesis of chelonian

shell and to a possibility of its alternative interpretation. Owing to the lack of direct paleontological data now there is only one way to understand the nature of the shell, namely, study of its development in recent turtles.

MATERIAL AND METHODS

Complete ontogenetic series of histological and total preparations of turtles were studied. They included more than 450 embryos and early postembryos of *Emys orbicularis* (L.), Emydidae; *Testudo graeca* L., Testudinidae; *Trionyx sinensis* Wiegmann, Trionyichidae. All the material was taken from the collection of the Department of Vertebrate Zoology at the St. Petersburg University. The embryos were sacrificed in 4% formalin. The stages of their development were determined after Yntema (1968). Histological sections approximately 10, 15, and 20 µm in thickness were stained with hematoxylin/eosin and azan/azocarmine; total preparations were stained with alizarin. Dry skeletons were used too. The terms of horny and bony parts of the shell (Fig. 1) are used after Zangerl (1969).

¹ Department of Vertebrate Zoology, St. Petersburg State University, Universitetskaya nab., 7/9, St. Petersburg 199034, Russia.

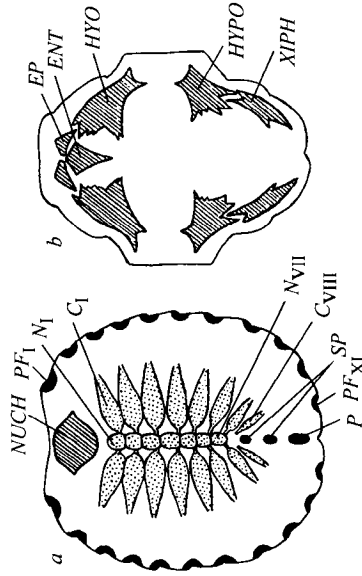


Fig. 1. Diagrammatic representation of the position of shell ossifications in juvenile *Emys orbicularis*: a) carapace, b) plastron. Abbreviations: C) costal plate, ENT) entoplastron, EP) epiplastron, HYO) hypoplastron, HYP) hypoplastron, N) neural plate, NUCH) nuchal plate, P) pygal plate, PF) peripheral plate, SP) suprapygal plate, XIPH) xiphoplastron. I - XI are the numbers of the plates. The plates developing on the basis of the internal skeletal elements are dotted, the plates representing the basic dermal elements are shaded, the plates which are homologized as osteoderms are black.

RESULTS

Complete data on the morphogeny of the bony shell in *E. orbicularis*, *T. graeca*, and *T. sinensis* was presented in some of my previous papers (Cherepanov, 1984, 1988, 1989 - 1992, 1994a, 1994b, 1995, 1996). It allows me to dispense with long morphological descriptions giving only a little information necessary for discussion.

In the species observed the development of the neural and costal plates is essentially similar. These bony plates form in the following way. By the 17th embryonic stage the body of the turtle embryo is flattened dorsoventrally, the trunk myomeres are mostly reduced, the dorsal dermis is thickened. Cartilaginous thoracic ribs and neural arches of vertebrae are sunken into the dermis. At stages 19 - 20 the cartilage of the internal skeleton becomes covered by a thin layer of perichondrial bone. As the hatching is approached, on the portions penetrated into the skin the bony perichondrium of the thoracic ribs and neural arches forms small spicules of bone (bony trabeculae) extending inside the dermis (Fig. 2a, b). The further expansion of these bony trabeculae results in formation of the neural and costal plates which at any stages of development are inseparably connected with the vertebrae and ribs giving them birth.

The primordium of the nuchal plate is first visible at stage 17 in *T. sinensis* and at stage 19 in *T. graeca* and *E. orbicularis*. There is only a wide accumulation of mesenchymal cells in the middle level of the dermis at the time. The primordium is situated within the anterior ridge of the dorsal disc (carapace) ahead of (*E. orbicularis*, *T. graeca*) or just over (*T. sinensis*) the muscle testospinalis cervicis (Fig. 2c). Osteogenesis in the nuchal primordium begins one stage later. The bony nuchal arises from a pair of symmetrical ossification centers in *T. sinensis* or as a result of chaotic ossification (without obvious centers) in the other species under study.

In *E. orbicularis* and *T. graeca* the lateral and caudal parts of the carapace include peripheral, suprapygal and pygal plates (in *T. sinensis* these ossifications are absent). All these elements originate in the dermis. Mesenchymatous primordia of the peripherals and the pygal are evident at the hatching stage. The peripherals are strictly located under the anterolateral boundaries of the marginal shields (Fig. 3a), the pygal — under the supracaudal shield in *T. graeca* but under the furrow separating the last pair of marginal shields in *E. orbicularis*. Primordia of the suprapygals appear by the age of three months. In normal development, the suprapygals lie along the midline of the carapace: the 1st — under the IV-th intervertebral furrow (approximately upon the IX-th trunk vertebra), the 2nd and the 3rd — under the V-th vertebral shield. Later, the spinous processes of trunk vertebrae number IX and sometimes number X form the sutural contacts with the 1st suprapygal plate.

Primordia of the plastral plates are indicated within the peripheral thickening of the ventral dermis at stage 16. At the beginning there are hyo-, hypo- and xiphoplastra which are situated in the middle stratum of the dermis. The hyo- and hypoplastra originate in the bridge region and lie near the place of dermal fixation of pectoralis and abdominalis lateralis muscles accordingly. The xiphoplastra are located within the posterior portion of soft plastral ridge just opposite the ventro-lateral projection of the pubis. The other plastral plates appear at stage 17 in the deepest dermal layer. The epiplastra develop inside the anterior part of plastral dermis just opposite the deltoideus muscle (Fig. 3b). The entoplastron is situated behind the epiplastra and represented by a pair of bony primordia separated at the midline. By stage 19 the left

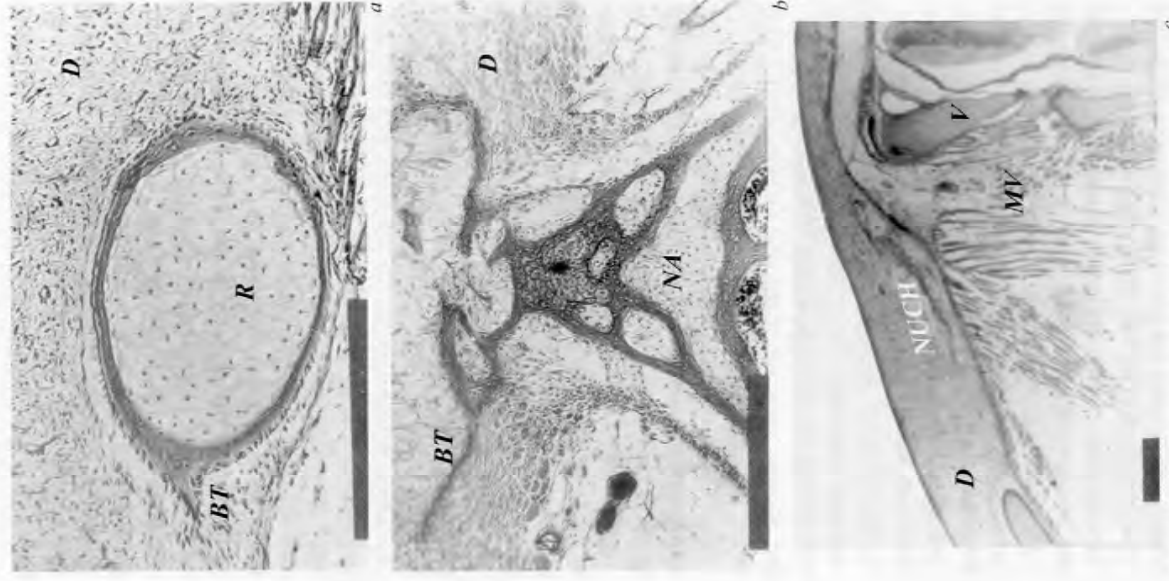


Fig. 2. Histological sections of embryos of *Testudo graeca* (a, b) and *Trionyx sinensis* (c): a) parasagittal section in the costal plate area, stage 22; b) transversal section in the neural plate area, stage 25; c) transversal section in the nuchal plate area, stage 19. Abbreviations: BT) bony trabecula, ED) epidermis, D) dermis, MN) neck muscles, NA) neural arch, R) rib, V) vertebra. Scale bar is 300 μ m. Other abbreviations are as in Fig. 1.

and the right parts of the entoplastron become fused (Fig. 3c).

The histological structure of the bony plates (with the exception of neurals and costals) develops in four successive stages. Stage 1 — the formation of the ac-

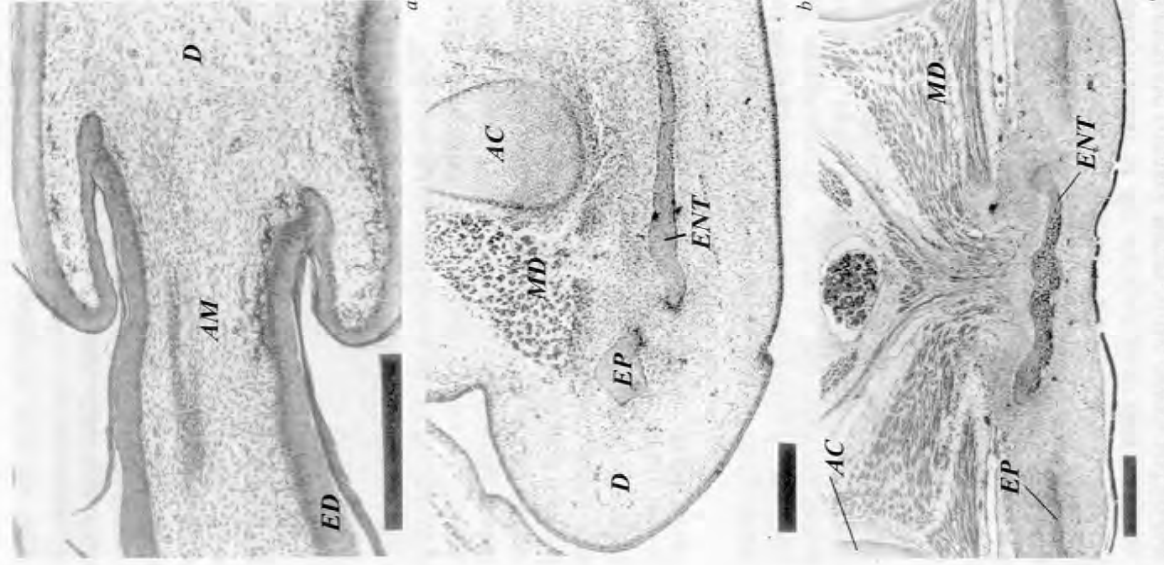


Fig. 3. Histological sections of embryos of *Emys orbicularis* (a) and *Testudo graeca* (b, c): a) parasagittal section in the peripheral plate area, stage 24; b) parasagittal section of the anterior portion of the plastron, stage 19; c) transversal section in the region of the epiplastron, stage 19. Abbreviations: AC) acromion, AM) accumulation of mesenchyme, MD) muscle deltoideus. Other abbreviations are as in Figs. 1, 2.

cumulation of mesenchymatous cells within the dermis. Stage 2 — the appearance of the ossification center inside the accumulation and the formation of a primary bony lamina; generally, the source of the plate basal layer. Stage 3 — the formation of the spongy

the ribs because the reorganization of the dermis takes place only near the rib and the beginning of this process conforms to the time of appearance of perichondrial bone expansion. Therefore, Kálin's observation cannot be used as a basis for wide phylogenetic reconstruction.

Zangerl (1939, 1969) and following in his footsteps Suzuki (1963) reduced the problem of the origin of the costals and neurals to the question about the cell sources of perichondrial ossification. They assumed that the bony cover around the neural arches and ribs on the portions sunken into the dermis are formed by osteoblasts of dermal nature. The principal critique of this view was given by Borkhvardt (1978). In particular, this author showed that, at least, the perichondrial bony lamina of the neural arches arose simultaneously as a single and indivisible structure located both on the cartilage portion which had penetrated into the dermis and on the portion outside the dermis. Our data confirm this observation. In addition, I subscribe to Borkhvardt's opinion by that in fact the problem of the origin of the osteogenetic cells bears little relation to the problem how closely the neurals and costals are attached to the axial skeleton. All the known embryological as well as comparative data do not give reason to suppose that these plates had independent development from the vertebrae and ribs in the past. As it was observed during turtle ontogeny, the neurals and costals originate as outgrowing perichondrial bones of the neural arches and ribs sunken into the dermis (Fig. 2*a, b*). There is no sound reason to assume that the morphogenesis of these plates in ancient turtles developed in any other way. Most probably, the turtle ancestors have formed their bony armor by means of insertion of the transformed elements of the axial skeleton (vertebrae and ribs) into the shell.

Some authors (Williams and McDowell, 1952; Romer, 1956; Sukhanov, 1964; Zangerl, 1969; Walker, 1973) believe that the plastral plates in turtles are formed from two different sources: the internal parts of the plates are homologous to clavicles, interclavicle and gastralia of the basic reptilian skeleton, and their external parts are more superficial dermal ossifications fused with the internals. First of all, this idea is based on the discovery of two levels of dermal ossifications (thecal and epithecal) in the marine turtle *Derموchelys coriacea*. Another argument in favor of the complicated origin of the plastrals is lack of congruence between the rod-shaped internal and wide exter-

nal parts of these bony elements in Triassic *Proganochelys* (Romer, 1956; Walker, 1973) but most evidently in the recent Trionychidae (Zangerl, 1969). Finally, a myth has existed for a long time that the internal (thecal) and external (epithecal) parts of the plastral plates have primary separate development during ontogeny of the trionychid turtles (Zangerl, 1939, 1969). However, precise study of the morphogenesis of bony plates in *Trionyx sinensis* showed, that no independent epithecal ossifications were present over the typical bony primordia at any stages of ontogeny (Cherepanov, 1995, 1996; Ivanov et al., 1995). The unusual superficial bony callosities in the shell of this turtle are only outgrowths of the common plates (thecal in Zangerl's terminology) inside the uppermost strata of the dermis. The morphological differences between the internal and external parts of the bony elements are predetermined by preliminary delamination of the trionychid dermis into histologically different layers, that is not evident in most of the other turtles.

In *Emys*, *Testudo*, and *Trionyx* as well as in other species observed so far (Vallen, 1942) each plastral plate is formed from a single primordium; except for the entoplastron, which originates from a pair of symmetrical (left and right) ossification centers. Thus, the idea of a complicated origin of the plastrals is refuted by their morphogenesis in living turtles. The early stages of plastron development in Testudines resemble that of cutaneous ossifications in the shoulder girdle (clavicles and interclavicle) and in the gastral skeleton of other reptiles (Cherepanov, 1984), that confirms the opinion of their complete homology. The most acceptable view on the ancestral state of the chelonian plastron is that it was formed by the dermal shoulder girdle and gastralia expanded inside the dermis (Fig. 3*b, c*). It is necessary to note that the insertion of girdles into the ventral armor is not characteristic of turtles exclusively. For example, similar structural complexes are obvious in ancient labyrinthodonts and plesiosaurs (Romer, 1956).

A simple (noncomplicated) dermal nature of peripheral, suprapygial, and pygal plates is not subjected to question now. The most common features of these shell ossifications are their late appearance in ontogeny, the formation of these bony plates in well-developed dermis and, as a rule, the determination of their place by the position of epidermal structures (in particular, horny furrows) which have appeared ear-

lier (Cherepanov, 1988, 1989 – 1992). The correlation between horny scutes and bony plates is most obvious in the marginal region of the carapace because the places of the origin of the peripheral plates strictly correspond to the position of the horny furrows bounding the marginal shields (Fig. 3a). If the horny furrows are absent over a large area of the shell, the bony plates discussed are irregularly located and their number is rather variable (for example, the suprapygals in typical turtles, the peripherals in *Lissemys* or do not develop at all (as in *Trionyx*). So, the peripherals, pygal and suprapygals of turtles have no morphogenetic differences from the osteoderms of other reptiles.

The nuchal plate is of great significance in the turtle shell. This large ossification is situated on the anterior border of the carapace and attaches the shoulder girdle and neck muscles (Fig. 2c). There are two principally different hypotheses concerning the origin of the nuchal plate. On the basis of the embryonic position of the plate and its development from a pair of primordia, it has been suggested, that the chelonian nuchal is a fusion of a pair of supracleithralia of the primary tetrapods (Vallen, 1942). On the other hand, the idea about the nuchal being a neomorph (not a modification of an old structure) exists too (Ivashchenko, 1987). Such a view is supported by some paleontological data. In particular, the presence of the sutural osteodermal complex over the shoulder girdle in pareiasaurs allowed the assumption that phylogenetically the chelonian nuchal had arisen from an analogous series of osteoderms through their consolidation.

The present ontogenetic study shows that the nuchal primordium originates at embryonic stages 17 – 19, practically at the time of appearance of the internal skeleton and musculature and in connection with them. Probably, the high phylogenetic and individual stability of this bony plate and the plastral elements is conditioned by strict morphogenetic correlations in the skeletal-muscular system of turtles (Cherepanov, 1994a). These peculiarities distinguish the nuchal plate from the osteoderms of reptiles, the osteoderms appear much later in ontogeny (hatching or early postembryonic stages) and their position is mainly determined by the location of the epidermal scutes (Cherepanov, 1988, 1989 – 1992). However, I am not sure that the nuchal is modified primitive supracleithralia. It is more likely that the element is a

neomorphic structure which developed in connection with the formation of muscles, the neck retractors, as a backing for them. In this context we should mention the opinion voiced by Sikorska-Piwowska (1985) that the ancient *Proganochelys* had no nuchal plate because there was not any mechanism of neck retraction in this form. So, primordially, the chelonian nuchal is unlikely to be an osteodermal complex.

As it was shown by the morphogenetic data each bony plate in the turtle shell is formed from a single source. In spite of high potentiality of the dermis to ossify and usual immobilization of the shell ossifications the fusion of the bony elements is not a typical phenomenon for turtles. In normal ontogeny it occurs at the early embryonic stages as a union of ossification centers inside the single mesenchymatous accumulation (for example, in the entoplastron or nuchal plate). During the postembryonic period fusions of bony plates are practically absent owing to the formation of well-developed periosteal coverings which separate the adjacent ossifications. The special exception is the fact of knitting of the hyoplastron with hyoplastron in *Lissemys*, *Cycloderma*, and *Cyclanorbis*, which is conditioned by the unique histological structure of the dermis in trionychids (Cherepanov, 1996). The other exception are rare abnormal individuals demonstrating fusions of plates in the regions of mechanical injury (Cherepanov, 1994a). The restriction of potentiality to the fusion of the bones has an important functional significance for turtles because at the expense of this the growth zones of all separate ossifications are preserved inside the consolidated shell structure.

So, according to the morphogenetic data the idea, that the turtle shell originated in phylogeny as a result of fusion of osteoderms with the elements of the internal skeleton, is the least probable. There are two other possible ways of shell formation. The first is the reduction of the primary osteoderms simultaneously with the expansion of more internal bones into the dermis (Deraniyagala, 1930). However, such a way is difficult to explain from the functional point of view because it is not clear what could be the reason for the transfer of the protective function from the osteodermal armor to the internal skeleton. In addition, it is rather questionable that the processes of reduction of some ossifications and expansion of others could take place in the dermis at the same place and at the same time. At least, we do not observe that in turtles. For

example, in marine forms all the bony plates of the reducing shell, in spite of the differences in their nature, are involved in this process. It may be that the process of bone reduction and the process of bone expansion have to be separated in time because of morphogenetic courses. In this connection, it is more reasonable to assume that the immediate ancestors of turtles were not armored animals (Gauthier et al., 1988). The formation of the chelonian shell should have been evolved in a unique evolutionary way (Fig. 4), which is reflected in their ontogeny. The dorsal disc was formed by modified neural arches and ribs, the ventral disc — by dermal elements of the shoulder girdle and, probably, the gastralia. Only the periphery of the shell consists of small ossicles resembling reptilian osteoderms. These ossifications developed in turtles as a connection between the dorsal and ventral discs, uniting these parts into a rigid shell.

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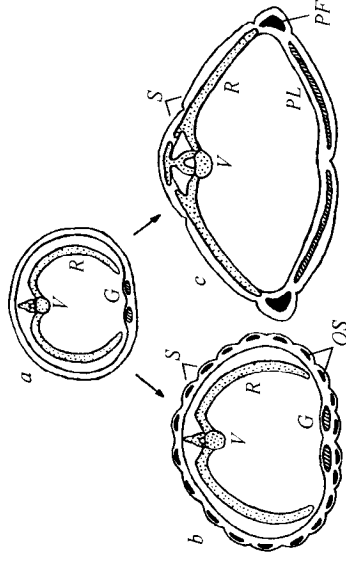


Fig. 4. Diagrammatic cross-section through the body of different reptiles demonstrating two ways of formation of bony armor: a) assumed primary unarmored condition, b) general reptilian armored condition, c) chelonian armored condition. Abbreviations: G) gastralia, OS) osteoderm, PL) plastral plate, S) horny scute or shield. Other abbreviations are as in Figs. 1 – 3.

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