

ONTOGENETIC DEVELOPMENT OF THE SHELL IN *Trionyx sinensis* (TRIONYCHIDAE, TESTUDINATA) AND SOME QUESTIONS ON THE NOMENCLATURE OF BONY PLATES

G. O. Cherepanov¹

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The embryonic and postembryonic development of the bony shell in *Trionyx sinensis* (Trionychidae) is observed. There are two main types of ossifications in trionychid armor, like in other turtles. Ossifications of the first type (neurals and costals) are modified elements of axial skeleton. Ossifications of the second type (nuchal, preneural, plastrals) are dermal bones developing independently from the internal skeleton. Hypotheses on the special epithelial origin of bony callosities as well as on the unique nature of anterior neural and plastral plates in Trionychidae do not confirm by morphogenetic data.

Key words: Trionychidae, bony shell, morphogenesis.

The arrangement of the bony shell in soft-shelled turtles (Trionychidae) has a lot of unique features. They characterize both the shell organization in general and the histological structure of its separate ossifications. These unique peculiarities were taken as basis of hypotheses about the special origin of the trionychid bony armor. As a result, there are numerous different opinions on the homology of the bony elements in trionychids (Williams and McDowell, 1952; Zangerl, 1969; Chkhikvadze, 1973; Meylan, 1984, 1987; et al.). However, the most of the hypotheses are based only on the comparative anatomical studies. The morphogenetic data which is so necessary for their examination are fragmentary and often contradictory. The present work is an attempt to fill in this flaw.

MATERIAL AND METHODS

The material under study includes more than 60 embryos and postembryos of *Trionyx sinensis* Wiegmann from the collections of the Department of Vertebrate Zoology at St. Petersburg University (VZ) and Zoological Institution of Russian Academy of Sciences (ZISP). The embryos were fixed in 4% solution of formalin. The stages of development were determined after Yntema (1968). The histological sections, approximately 10 and 15 μm in thickness, were

stained with hematoxylin and eosin, the total preparations were stained with alizarin. The dry unstained preparations were used too.

RESULTS

Embryos, Stages 16 – 17. The body is flattened dorso-ventrally. The derma is thick, homogeneous and consists of stellate cells. The internal skeleton is cartilaginous. The ribs, except the first pair, are sunk into the back derma. The neural arches of trunk vertebrae numbers II through IX are in contact to the derma. The other neural arches are separated from it with subdermal tissue. The anlagen of bony plates are first indicated as mesenchymatous accumulations inside the peripheral thickening of the ventral derma. At the beginning these are hypo-, hypo-, and xiphiplastra. The hypo- and hypoplastra originate in the bridge region near the place of dermal fixation of muscle pectoralis and muscle abdominalis lateralis, respectively. The xiphiplastra lie within the posterior portion of soft plastron just opposite the ventro-lateral projection of pubis. The other dermal bony elements are evident at Stage 17. The epiplastra arise inside the anterior part of plastral derma opposite the muscles deltoideus and testoscapuloprocoracoideus (Fig. 1a). The entoplastron is situated behind epiplastra and represented by a pair bony anlagen separated at the midline. The primordium of nuchal plate is paired too. It is formed within the carapacial derma in

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

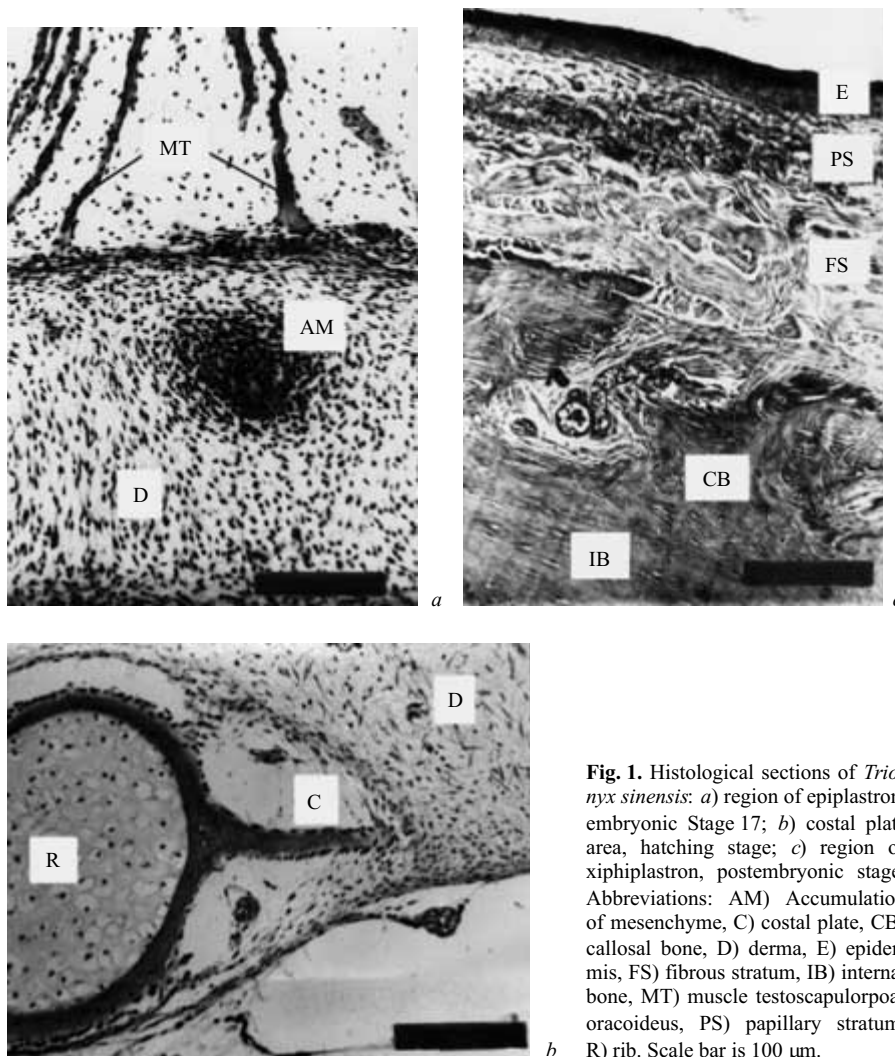


Fig. 1. Histological sections of *Trionyx sinensis*: a) region of epiplastron, embryonic Stage 17; b) costal plate area, hatching stage; c) region of xiphiplastron, postembryonic stage. Abbreviations: AM) Accumulation of mesenchyme, C) costal plate, CB) callosal bone, D) derma, E) epidermis, FS) fibrous stratum, IB) internal bone, MT) muscle testoscapulorpoaracoideus, PS) papillary stratum, R) rib. Scale bar is 100 μ m.

front of scapula just above the muscle testospinalis cervicis.

Embryos, Stages 19 – 21. The derma is differentiated. The fibroblasts and collagen fibers are visible in it. The perichondral ossifications appear on the elements of internal skeleton. The left and right anlagen of nuchal are fused. Now it is an arc-shaped perforated bony plate. The epiplastra are J-shaped with a long postero-lateral ramus (Fig. 2a). The entoplastron before paired becomes a single boomerang-shaped bone. The hyo-, hypo-, and xiphiplastra form long processes on their borders.

Embryos, Stage 22 – hatching stage. The derma is delaminated into the hypodermic, fibrous, and papillary strata. On the portions penetrated into hypo-

derma, perichondral ossifications of thoracic ribs (II – IX) and vertebrae (II – VIII) form bony trabeculae of anlagen of neural and costal plates (Fig. 1b). The nuchal is the largest ossification in the carapace. Its lateral wings touch the ribs of second pair and midposterior projection covers the anterior part of the neural arch of the first thoracic vertebra (Fig. 2b).

Postembryos, bony carapace is 45 – 110 mm long. The central part of carapace becomes consolidated. The little neuro-costal fontanel is preserved only in the smallest individuals. The first neural is round or oval. It is separated from the nuchal with a wide fontanel. The plastral plates contact each other, but only the hyo-hypoplastral union is sutural. The large fontanel is evident in the middle of the plastron.

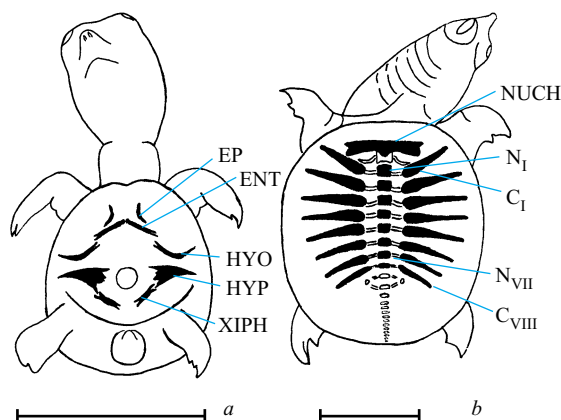


Fig. 2. Diagrammatic representation of the position of shell ossifications in *Trionyx sinensis*: a) ventral view, embryonic Stage 19; b) dorsal view, hatching stage. Abbreviations: C) Costal plate, ENT) entoplastron, EP) epiplastron, HYO) hyoplastron, HYP) hypoplastron, N) neural plate, NUCH) nuchal plate, XIPH) xiphoplastron. I–VIII are the numbers of the plates. Scale bar is 10 mm.

The expansions of bony elements within the fibrous and papillary strata of derma form superficial callosities (Fig. 1c).

Postembryos, bony carapace is 120 – 300 mm long. The carapace is consolidated nearly completely. The pair small round postnuchal fontanels is preserved for a much longer time. The configuration of the neural series is generally 6P-6P-6P-6P-4-6A in Pritchard's terminology (1988). The first neural is very long (Fig. 3a), the eighth one, if it is present, is partly reduced. The preneural is usually absent. The costals have long sutural contacts each other and ones of their first pair with the nuchal. The non-extended portions of ribs are short. The last pair of costals is united on the midline of the carapace. The central fontanel in the plastron can be divided into anterior and posterior portions by the medial processes of the hypoplastra.

DISCUSSION

The concept (Zangerl, 1969) that trionyhid bony armor as a fusion of two levels of dermal ossification (thecal and epithecal) is not confirmed by morphogenetic data. As observed during *Trionyx* ontogenesis, the superficial bony callosities are not separate epithecal ossicles at any stages of development but only outgrowths of the usual plates inside the uppermost strata of derma (Fig. 1c; Cherepanov, in press). The morphological differences between the internal

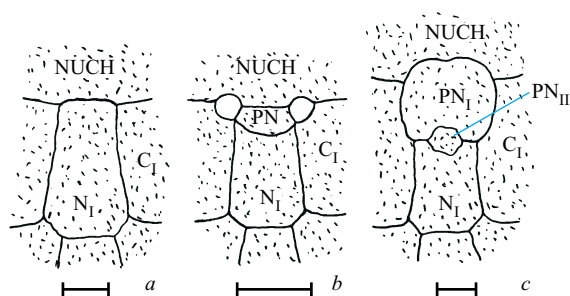


Fig. 3. Individual variants of the postnuchal region of carapace in *Trionyx*: a) *T. sinensis*, ZISP 16552; b) *T. sinensis*, ZISP 16560; c) *T. egypticus*, VZ 00260. Abbreviation: PN) Prenal plate. Other abbreviations are as in Fig. 2.

(rod-shaped) and external (callosal) parts of bony elements are conditioned by the strict delamination of trionyhid derma into the histologically different strata: hypodermic, fibrous and papillary (Cherepanov, 1992). Such dermal stratification is absent in the most of other turtles, that is why the structure of bony tissue of their armor is simpler.

A number of authors believe that phylogenetically neural and costal plates are cutaneous bones secondarily associated with vertebrae and ribs (see Zangerl, 1969). According to this idea, nearly all the bony plates lain on the midline of the carapace began to be considered elements of a neural series. With respect to soft-shelled turtles it has been suggested that the preneural plate found in the postnuchal area of carapace in many species is actually a first neural (Carpenter, 1981; Meylan, 1984, 1987; et al.). The statement is supported by the fact, the preneural in such turtles as *Lissemys* and *Cycloderma* lies directly above the first thoracic vertebra to which it is contacted. Developing this point of view Meylan (1987) changed the numeration of neurals in the trionyhid shell.

However, the concept of compound origin of the neurals and costals is refuted by their morphogenesis in living forms (Cherepanov, 1992b). During turtle ontogenesis these plates are formed as expansions of perichondral ossifications covering the neural arches of thoracic vertebrae and ribs (Figs. 1b, 2b). Thus, they are modified elements of the axial skeleton. On the contrary, the other plates of the shell, including preneural, are cutaneous bones because they develop as a result of ossification of dermal cell accumulations (Fig. 1a). Concerning the contact between the preneural and the first thoracic vertebra it is sutural and, therefore, secondary. So, the preneural plate in

Trionychidae as well as in other turtles is not true neural. A shape and quantity of the preneural are rather variable and they as individual abnormalities (Fig. 3*b, c*) are accessory plates (Cherepanov, 1994) inside the postnuchal fontanel. To my mind, there are no sound reasons to assume that in ancient turtles the bony plates developed in any other way. Therefore, the Meylan's terminology of neurals is likely to be not correct.

The majority of recent species of *Trionyx* has no preneural plate in normal. Their first neural is very long, occupying the place of preneural it contacts with the nuchal plate (Fig. 3*a*). This condition gave a basis to suggest that the anterior neural of *Trionyx* originates by fusion the primary preneural and first neural plates (Webb, 1962; Chkhikvadze, 1973). Some confirmation of this view have been presented by Carpenter (1981). He found the preneural plate in some juvenile and adult specimens of *Trionyx ferox*, moreover, the plate was relatively larger in the juveniles than in the adults. On this fact Carpenter concluded that the preneural is usually incorporated with the first neural during the *Trionyx* ontogenesis and, therefore, rarely preserved in the adult individuals as an independent ossification.

In spite of this conclusion is very disputable (in reality nobody observed the process of fusion mentioned above), the idea of complex origin of the anterior neural in advanced Trionychidae is widespread (Meylan, 1984, 1987; Chkhikvadze and Shuvalov, 1988; et al.). However, our research of *Trionyx* ontogenesis shows that normally there are no discrete ossifications within the derma between the nuchal and the first neural plates at any stages of development. The anlage of the first neural has primarily a round shape. Later, it gradually becomes elongated but exclusively as a result of own expansion. Thus, we can contend that the anterior neural of *Trionyx* develops from a single anlage and corresponds to the first neural plate only, like in other turtles.

Special attention should be taken to the hypothesis by Williams and McDowell (1952) on the nature of the trionychid plastron. According to that, in the soft-shelled turtles the actual entoplastron is absent, the plate usually termed entoplastron corresponds with combined epiplastra, and the pair anterior elements are neomorphs. Such interpretation is mainly based on the following conditions: the trionychid entoplastron is unique V-shaped, it arises as a paired element, it does not receive the acromio-plastral ligament, and it is more anteriorly placed than the ento-

plastron of other turtles. However, as Deraniyagala (1939) reported, the young individuals of *Lissemys punctata* have the entoplastron of T-shaped, which is typical for all Testudines. The plate becomes V-shaped only in the late ontogenesis due to a disappearance of the mid-posterior projection. It is interesting to remark, the similar entoplastron modifications are evident during phylogeny of Trionychoidea (Chkhikvadze, 1973; Nessov, 1977). The more anterior position of the entoplastron in trionychids as well as the loss of the acromio-plastral ligament are also connected with the reduction of its mid-posterior portion. That the entoplastron originates from a pair bony anlagen is not unique feature of trionychids. Such way of morphogenesis is general for any turtles (Vallen, 1942; Cherepanov, 1984, 1992*b*) and it cannot be used, as suggested by Williams and McDowell, to prove the special origin of the trionychid plates. Like some authors (Meylan, 1987), I consider that the bony elements of the trionychid plastron correspond to the ones of other turtles completely.

CONCLUSIONS

Two types of bony plates found in the shell of *Trionyx* are well distinguished by the way of morphogenesis. Ossifications of the first type (neurals and costals) are modified elements of axial skeleton, because they are formed in the derma as outgrowths of the perichondral bone of the neural arches and ribs. Ossifications of the second type (nuchal, preneural, plastrals) are cutaneous bones because they develop by an ossification process inside the accumulations of dermal cells. In spite of essential structural differences the nature of bony armor of Trionychidae is same to one of other turtles. The ontogenetic data confirm this view.

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