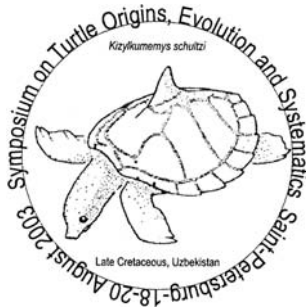# FOSSIL TURTLE RESEARCH

VOLUME 1

Proceedings of the Symposium
on Turtle Origins, Evolution and Systematics

August 18 – 20, 2003,
St. Petersburg, Russia

Edited by
Igor G. Danilov and James F. Parham

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**Cover photo: PIN 52-1a, holotype of *Yaxartemys longicauda* Riabinin, 1948,
Upper Jurassic of Kazakhstan, Karatau Ridge, vicinity of Mikhailovka village
Photograph: Igor Danilov**

ONTOGENESIS AND EVOLUTION
OF HORNY PARTS OF THE TURTLE SHELL

Gennady O. Cherepanov

Based on study of the ontogenetic development of typical turtles, it was found that anlages of horny scales of the shell develop at early embryonic stages as epidermal placodes (local thickenings of epidermis). The position of the placodes relates to body segmentation: the marginals arise opposite each myoseptum; the pleurals, vertebrals, and possibly plastral scales, originate over one myoseptum. The vertebral scales result from the fusion of primary paired anlages. The position of these anlages is determined strictly by the location of the previously arisen pleural placodes. Basic morphogenetic regularities of the horny shell development in turtles were formed in the earliest period of their evolution and preserved unchanged. The evolution of the horny shell mainly progressed towards a decrease in the number of its elements. This process took place as a result of the reduction and fusion of the scales or their anlages. The principal directions of the evolutionary development of the scalation in the turtle shell are discussed.

INTRODUCTION

The presence of horny scales is a typical feature of the turtle shell. The scales are present in most representatives of this reptilian order, including the oldest forms. Despite the fact that the scale mosaic of the shell has wide limits of interspecies (Zangerl, 1969) and individual (Zangerl and Johnson, 1957; Cherepanov, 1987, 1991b) variability, the principal model of the shell pholidosis, which formed in the Triassic, has remained universal and conservative throughout the history of the group. The reasons of this phenomenon possibly lie in the stability of morphogenetic processes determining this model. The absence of direct paleontological data on early stages of the turtle evolution requires that the main hypotheses about establishment of the scale mosaic are derived from the study of recent animals (Gadow, 1899, 1901; Newman, 1905; Deraniyagala, 1934; Grant, 1937a, b). However, these hypotheses are based mainly on data on individual variability of the shell scala-

tion, and so are often contradictory. Studies of the ontogenetic development of the turtle shell have been carried out only recently (Cherepanov, 1987–2005). These studies reveal morphogenetic mechanisms of the control of the scalation and causes of different deviations from the normal condition. Moreover, these data may have phylogenetic utility, and in particular they may shed light to the problem of origin of the horny shell of turtles.

MATERIAL AND METHODS

The work is based on a study of serially-sectioned specimens that document the embryonic development of *Emys orbicularis* (Emydidae) and *Testudo graeca* (Testudinidae). The developmental stages were determined according to Yntema (1968). The material was preserved in 4% formaldehyde. Embryos were dehydrated in an ethanol series and embedded in paraffin. The transverse, frontal and sagittal histological sections of 10, 15 and 20 μm were stained by hematoxylin with eosin and asan with asokarmin. The number of specimens under study is 24 embryos of *E. orbicularis* and 50 embryos of *T. graeca*. Variability in the horny shell in turtles was studied on the basis of

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collections of the Zoological Institute of Russian Academy of Sciences, St. Petersburg (ZIN) and St. Petersburg State University (SPSU), including more than 1000 specimens of 60 genera (see Cherepanov, 2005). Nomenclature of horny elements is given according to Zangerl (1969), with some additions (Fig. 1).

RESULTS

The development of the scale mosaic in the ontogeny of turtles has been described in details in previous publications (Cherepanov, 1987, 1992, 2005); therefore, it is not required to present a detailed account of morphogenetic data here. As the development of the scalation in the studied species is very similar, only its description in *T. graeca* is given below. Some peculiarities of the scalation development in *E. orbicularis* are noted separately.

The first anlages of the horny elements of the shell appear at Stage 13. At this stage, the body

of the embryo is laterally compressed and forms two large longitude protrusions, slightly above the limb buds — the left and right marginal folds (= carapace ridges). The integument forms septal invaginations on the lateral sides of the body. The epidermis is 1–2 cell layers thick. It is underlain by a thin layer of dermis. The septal invaginations of the marginal folds have small local thickenings of the epidermis, the anlages of marginal scales (= marginal placodes). Four additional pairs of epidermal thickenings, which represent anlages of pleural scales (pleural placodes), are present above the marginal folds, at the level of neural tube. They positioned in II, IV, VI and VIII trunk septal invaginations, which located opposite to transverse myosepta same numbered (the first trunk septal invagination is located opposite to transverse myoseptum, where the first trunk rib appears later) (Fig. 2A, B). In the area of the placodes, the epidermis is three cell layers thick and its basal cells are cylinder-shaped.
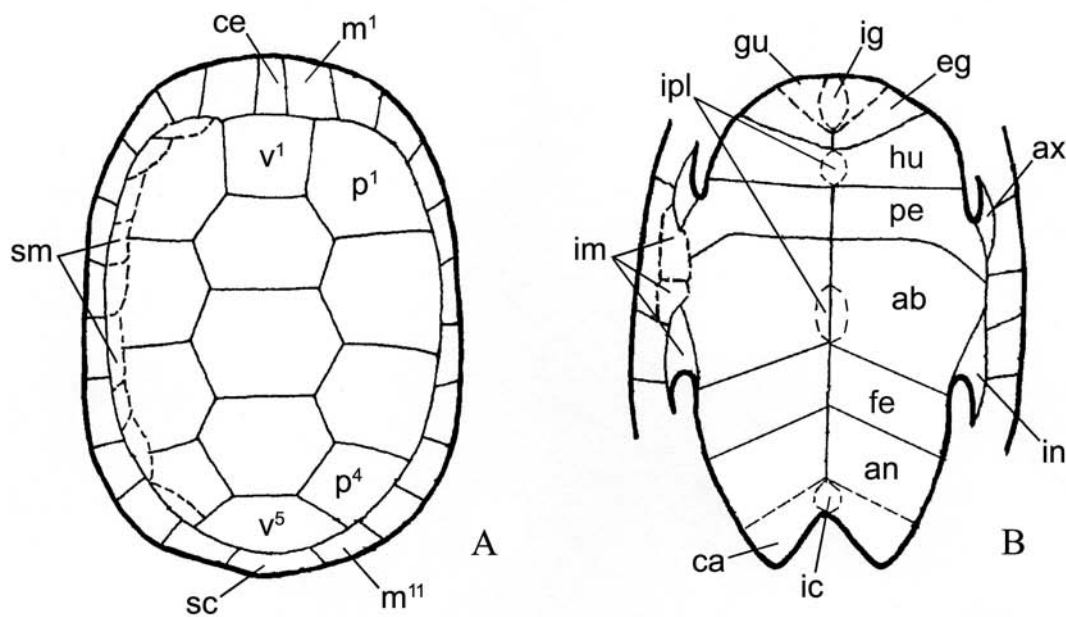
Fig. 1. Nomenclature of the horny scales of the turtle shell: A – carapace, B – plastron. Abbreviations: **ab**, abdominal; **an**, anal; **ax**, axillary; **ca**, caudal; **ce**, cervical; **eg**, extragular; **fe**, femoral; **gu**, gular; **hu**, humeral; **ic**, intercaudal; **ig**, intergular; **im**, inframarginal; **in**, inguinal; **ipl**, interplastral; **m**, marginal; **p**, pleural; **pe**, pectoral; **sc**, supracaudal; **sm**, supramarginal; **v**, vertebral; **1–11**, numbers of the scales.
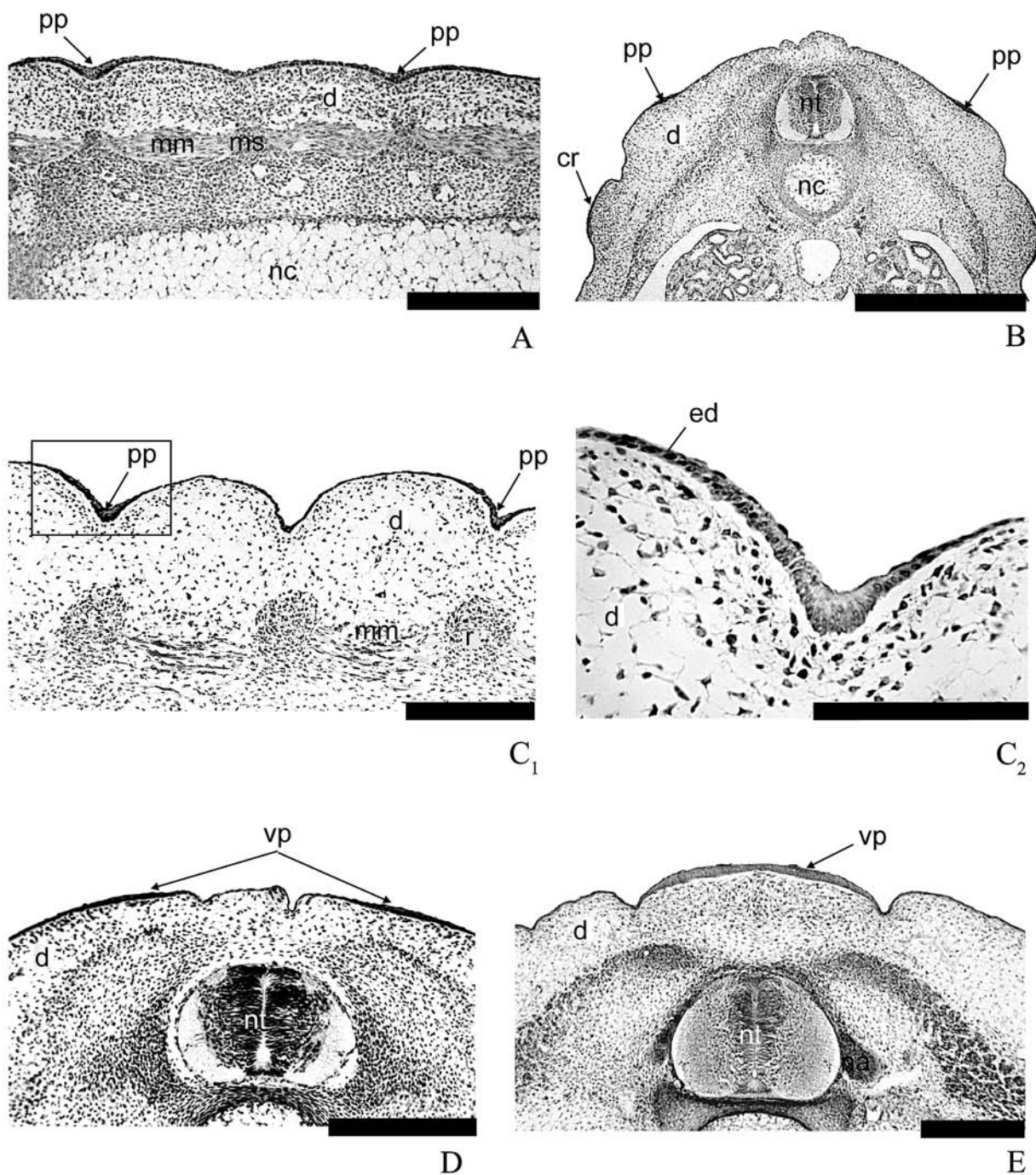
Fig. 2. Cross sections of embryonic *Testudo graeca* in the dorsal area: A – frontal section on the level of notochord, Stage 13; B – transversal section, Stage 15; C – parasagittal section in the region of the 4–6-th ribs, Stage 15; D – transversal section in the mid-dorsal region, Stage 15; E – transversal section in the mid-dorsal region, Stage 16. Scale bars are 100 μm (C$_2$), 250 μm (A, C$_1$, D, E), 500 μm (B). Abbreviations: **cr**, carapace ridge; **d**, dermis; **ed**, epidermis; **mm**, myomere; **ms**, myoseptum; **na**, neural arch; **nc**, notochord; **nt**, neural tube; **pp**, pleural placode; **r**, rib; **vp**, vertebral placode.

At Stage 15, twelve pairs of marginal and four pairs of pleural placodes are clearly visible (Fig. 3A). The marginal and pleural placodes are separated by narrow and wide intervals of thin epidermis, respectively (Fig. 4A–D). The pleural placodes are asymmetrical (Fig. 2C). In *E. orbicularis,* they have a shape of spherical cell accumulations (Fig. 4A). Dorsal to the pleural placodes, 5 pairs of new epidermal thickenings are visible, which represent anlages of vertebral scales (= paired vertebral placodes). They are situated symmetrically on each side of the body, on the level of transverse trunk myosepta I, III, V, VII and IX; the left and right anlages are separated along the midline by a narrow band of thin epidermis (Fig. 2D).

By Stage 16, the body of the embryo is rounded in the transverse section. The marginal folds of both sides are fused at the midline, anteriorly and posteriorly, surrounding the carapace. The dermis layer is distinctly thickened. The septal invaginations are relatively weakly developed (Fig. 4E). A small cervical placode appears in the cranial part of the carapace. A wide supracaudal placode appears in the caudal part of the carapace as a result of fusion of marginal placodes XII (in *E. orbicularis* the marginal placodes XII are not fused). The left and right anlages of the vertebral placodes are fused in pairs along the midline of the carapace (Fig. 2E). In the ventral part of the body, the dermis is thickened at periphery and forms the soft-cutaneous plastron (Fig. 3B). There are six pairs of symmetrical epidermal thickenings, anlages of the plastral scales (= plastral placodes).

At Stage 17, the body of the embryo is dorsoventrally flattened. The scale anlages are wide (they lose the placode shape) and exhibit variable thicknesses of the epidermis. The anterior margins of these anlages have become progressively thinner, whereas the posterior and posterolateral margins form sharp borders with thin epidermis. Along these borders, directly under the basal membrane, there are narrow accumulations of dermal cells (Fig. 4F). Later, the epidermis above these accumulations submerge in the dermis,
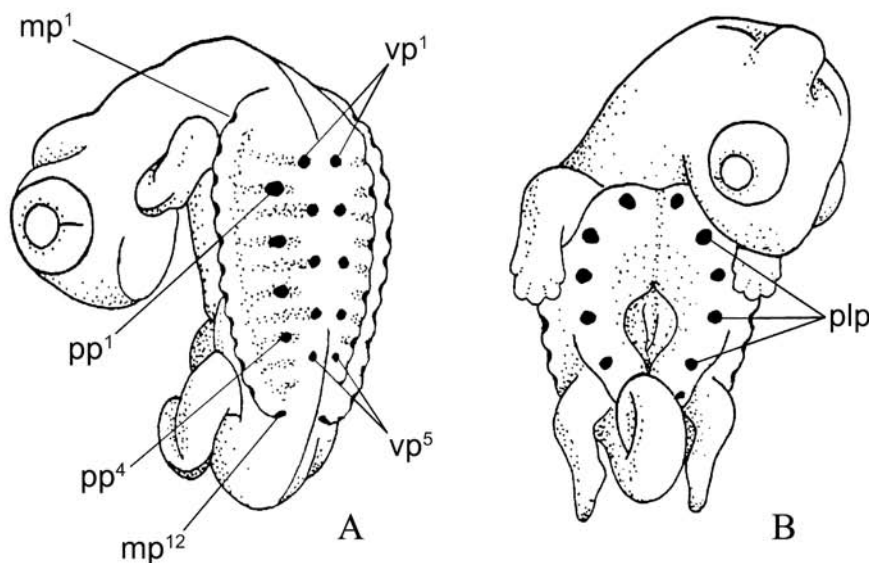
Fig. 3. Scheme of the position of epidermal placodes (= scale anlages) in embryos of *Emys orbicularis*: A – dorsal view, Stage 15; B – ventral view, Stage 16. Abbreviations: **mp**, marginal placode; **plp**, plastral placode; **pp**, pleural placode; **vp**, vertebral placode; **1–12**, numbers of the scales.
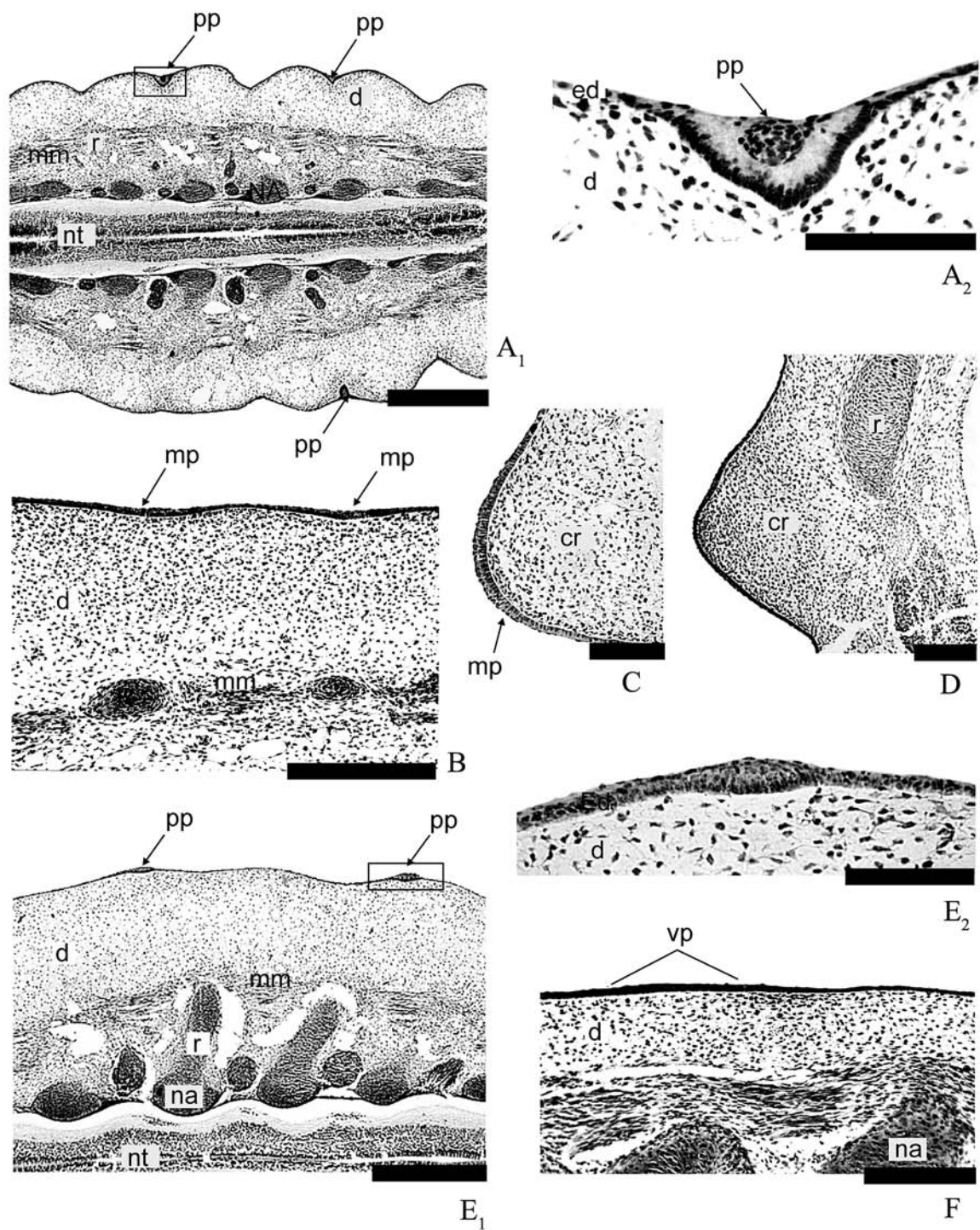
Fig. 4. Cross sections of embryonic *Emys orbicularis* in dorsal and lateral areas: A – frontal section on the level of the neural tube, Stage 15; B – frontal section through the carapace ridge, Stage 15; C, D – transversal sections through the carapace ridge, Stage 16; E – frontal section on the level of the neural tube, Stage 16; F – parasagittal section in the vertebral region, Stage 16. Scale bars are 100 µm (A_2, C, D, E_2), 250 µm (B, F), 500 µm (A_1, E_1). Abbreviations are on Fig. 2.

forming the anlages of the scale sulci, which separate (although not completely) the shell scales. In the carapace, the anlages of intervertebral and intermarginal sulci are first to appear. Then the anlages of vertebral-pleural and interpleural sulci appear. In the plastron, the anlages of all sulci, including the medial one, originate at the periphery, nearly simultaneously.

By Stage 19, the process of the formation of the scales is almost completed. The fused sulci surround the scales from all sides. There are one cervical, five vertebral, four pleural, 11 marginal, and one supracaudal scales in the carapace (in *E. orbicularis* the supracaudal scale is absent and the twelfth pair of marginals is present), six pairs of plastral, and two pairs of inframarginal scales in the plastron.

During subsequent stages of embryogenesis, the hornification and formation of the definitive structures of the epidermal shell (horny scales and sulci) take place.

DISCUSSION

Morphogenetic regularities of the horny shell ontogenesis in turtles – Study of the development of the epidermal shell in *E. orbicularis* and *T. graeca* reveals morphogenetic regularities that determine the succession of scale formation in two species, as well as the general model of pholidosis for turtles. These regularities may be summarized as follows:

1. The anlages of the horny scales appear at early embryonic stages as local thickenings of epidermis (i.e., placodes; Fig. 3). In the carapace, and probably in the plastron (see below), the placodes are confined to areas of transverse trunk myosepta, which are marked by septal invaginations on the sides of the body. Thus, it may be concluded, that the position of the horny scales is determined by the primary segmentation of the embryo.

2. The marginal placodes appear in each segment (i.e., in each septal invagination of the marginal folds; Fig. 4B); their number (12 pairs) corresponds to the number of myosepta, separating myomeres of the carapace. Therefore, the number of marginal scales is determined by the number of segments forming the carapace.

3. The pleural placodes (4 pairs) are formed symmetrically on each side of the body (Fig. 2B; see also Burke, 1989, fig. 1). They are situated in areas of even (II, IV, VI, VIII) trunk myosepta. Thus, unlike marginal placodes, the pleural placodes are situated not in, but over, each septal invagination (Figs. 2A, C; 4A). It should be mentioned that there are no morphological differences between areas of adjacent myosepta (with placodes or without them). It is possible that segments, connected with placodes in normal conditions, are not fully determined. This may explain the very high variability of the scalation in the pleural area of the turtle shell (Zangerl and Johnson, 1957).

4. The vertebral placodes appear later than the pleural ones as paired (left and right) anlages (Fig. 2D). They are situated in the dorsal part of the carapace in areas of odd (I, III, V, VII, IX) trunk myosepta (i.e., in staggered order with the pleural placodes). The position of the anlages of the vertebral placodes is determined by the position of the pleural placodes. The correlation between the anlages of the pleural and vertebral placodes on one side of the body is more stable than the correlation between two anlages of one vertebral placode. This is indicated by data on aberrant development. In the case of the asymmetrical position of the pleural placodes, left and right anlages of the vertebral placodes also develop asymmetrically, but in a way that the staggered order of the alternation the pleural and vertebral placodes is retained on each side of the body (Cherepanov, 1987).

5. The plastral placodes (6 pairs) appear later than the anlages of the carapace scales. They are laid on the periphery of the plastron primordium, symmetrically on each side of the body. The places of their appearance are not clearly connected with

the position of the myosepta; however, indirect evidence allows one to assume such a connection.

First, the periphery of the plastron has some features of segmentation at early stages of ontogenesis (Yntema, 1970). Second, as all scales of the shell (both carapace and plastron) exhibit the same type of development, and it might be suggested that the strict order of their arrangement has the same cause (Cherepanov, 1991a). Additionally, there are a number of arguments supporting the idea that the anlages of plastral scales are situated not in each, but over one segment. These arguments include the following peculiarities of the plastron structure: 1) the number of plastral scales is half the number of marginals, which are situated in each segment; 2) the plastral scales are similar in size to pleural scales, either of which occupies two adjacent segments; and 3) in the area of the bridges, the pectoral and abdominal scales of the plastron contact two marginal scales each.

6. The placodes have a capacity to expand independently. This expansion may be different in different directions, making the shape of each placode asymmetrical (Figs 2C, 4E). The growth is progressed mainly in thinner parts of the placodes and, probably, as a result of thickening of the epidermis at these thin-layer areas. During development, the thin-layer interplacode zones are narrowed, and the expanded scales gradually occupy the entire external surface of the shell. The primary type of growth of the scales is retained in turtles throughout their life, and is expressed in different thicknesses of growth lines on periphery of horny elements.

7. The sulci separating shell scales are formed in ontogenesis as local (isolated) submergences of epidermis to the dermis. Their anlages are confined to areas in which there is a dramatic change of the epidermis thickness (mainly along the posterior and posterolateral borders of the placodes). Later, the anlages of the sulci expand along the border between regions of thick and thin epidermis, and join together to form an entire system.

This morphogenesis results in sinuous-shaped sulci and extremely high variability of their contacts with each other (Tinkle, 1962). This is connected with the observation that the size of scale anlages is not strictly determined unlike their places of appearance. Differences in the size of scales are well demonstrated by the variability of plastral formulae (Lovich and Ernst, 1989).

Evolution of the horny shell in turtles – As mentioned above, the appearance of the scale anlages in turtles takes place exclusively at the areas of the transverse myosepta that separate the trunk myomeres. For this reason, turtles may have no more than one transverse row of scales per segment, whereas the maximum possible number of scales in one longitude row equals the number of segments in which the row is formed, and may barely exceed it. This peculiarity of the pholidosis in turtles is supported by numerous data on variability of scalation in recent and fossil forms (Newman, 1905; Deraniyagala, 1939; Zangerl and Johnson, 1957; Cherepanov, 1987; and others).

Based on these morphogenetic data and the observations of other authors (Hay, 1898; Gadow, 1899; Newman, 1905; Deraniyagala, 1934), it seems that the ancestors of turtles had horny scales in the all longitudinal rows corresponding to the number of segments, in similar fashion to these marginal scales of living forms. This state of pholidosis is the most polymeric. The epidermal shell could progress only towards a reduction of the number of elements, as is observed throughout the history of the group (Młynarski, 1976; and others). The oligomerization of the scalation is realized in two ways: 1) decreasing of the number of the transverse rows of scales as a result of reduction of the number of segments of the shell (compare ancient and recent turtles); and 2) decreasing of the number of scales as a result of their reduction and fusion. Study of the development of pholidosis in turtle evolution was used as a basis for establishing four successive levels of shell organization:

amphichelydian, mesochelydian, metachelydian, and neochelydian (Zangerl, 1969).

Unlike their probable ancestors, turtles are characterized by strongly shortened and immobilized trunk. Even among the oldest representatives of the order (*Proganochelys*) the number of trunk segments forming the shell is not high (16–17), as marked by the number of the marginal scales (Fig. 5A). In most recent turtles, the number of marginals is reduced to 12 pairs and is very stable. The immobility of the axial skeleton and development of the solid bony shell are responsible for the appearance of unusually large scales that cover several segments of the body. In this way the wide vertebral, pleural and plastral scales were formed. Later in the history of turtles, kinesis of the shell evolved. It is expressed in formation of hinges between separate parts of the shell (in places of coincidence of the borders of horny scales and bony plates), but does not result in changes in pholidosis. The hinges appear mainly in the plastron (*Kinosternon*, *Pelusios*, *Cuora*, *Emys*, and others), and are very rare in the carapace (e.g., *Kinixys*).

Reduction of the number of scales is the most significant process in the evolution of the turtle pholidosis. Scales under reduction are situated at the turn of the sulci and are usually small, diamond-shaped (e.g., the interplastral scales; Newman, 1905, figs. 45, 47), or triangular in shape (e.g., the axillary and inguinal scales of *T. graeca*). Another peculiarity of these small scales is their displacement in relation to normal (i.e., large) scales of the same longitude row. This phenomenon is mainly connected with the allometric growth of the scale anlages; as a result, the scale under reduction retains greater primary embryonic position—position of its epidermal placode. This is well demonstrated by scales of the plastral row, of which anlages are laid on the periphery of the plastron, and in which reduction looks like displacement from the medial zone of the plastron (Chkhikvadze, 1973; Hutchison and Bramble, 1981). It should be noted that, as a result of strict

determination of places of appearance of the scale anlages by trunk segmentation, the reduction of any scale leads to the intensification of growth of the adjacent ones, covering the vacant area. It is evident for anomalous specimens (Cherepanov, 1987, 1991b).

The processes associated with the transformation of individual scales operate over a considerable length of time and occur in different ways otogenetically. Thus, the scales under reduction demonstrate the following deviations in their development in comparison with scales that form in a more typical pattern (i.e., vertebral, pleural, marginal, and plastral scales): 1) diminishing the embryonic anlage of the scale in size and thickness, which is usually accompanied by a change in the timing of its appearance to a later ontogenetic stage (axillary and inguinal scales); 2) disappearance of the anlage of the sulcus, which leads to the formation of scale borders by the expansion of sulci of the adjacent scales (leading to the formation of additional interplastral scales in turtles, which do not have them in normal conditions); and 3) reduction of the rate of scale growth, which leads to a relative decrease of scale size at postnatal development (for example, the cervical scale in the Testudinidae).

Fusion of the horny elements is the second most significant process of pholidosis transformation in turtles. This can be recognized in ontogenesis in two ways. First, by the fusion of embryonic scale anlages (epidermal placodes) at the stage preceding the formation of the sulci between them. This is how the vertebral scales form in all turtles, and it is also how the single supracaudal scale in the Testudinidae is formed. Second, by the reduction of the formed horny sulci at later stages of ontogenesis. In this way the horny sulci disappear in juvenile *Carettochelys insculpta* (Zangerl, 1959, 1969).

In addition to the reduction and fusion of scales described above, other events might take place in the turtle ontogenesis. First, this is when
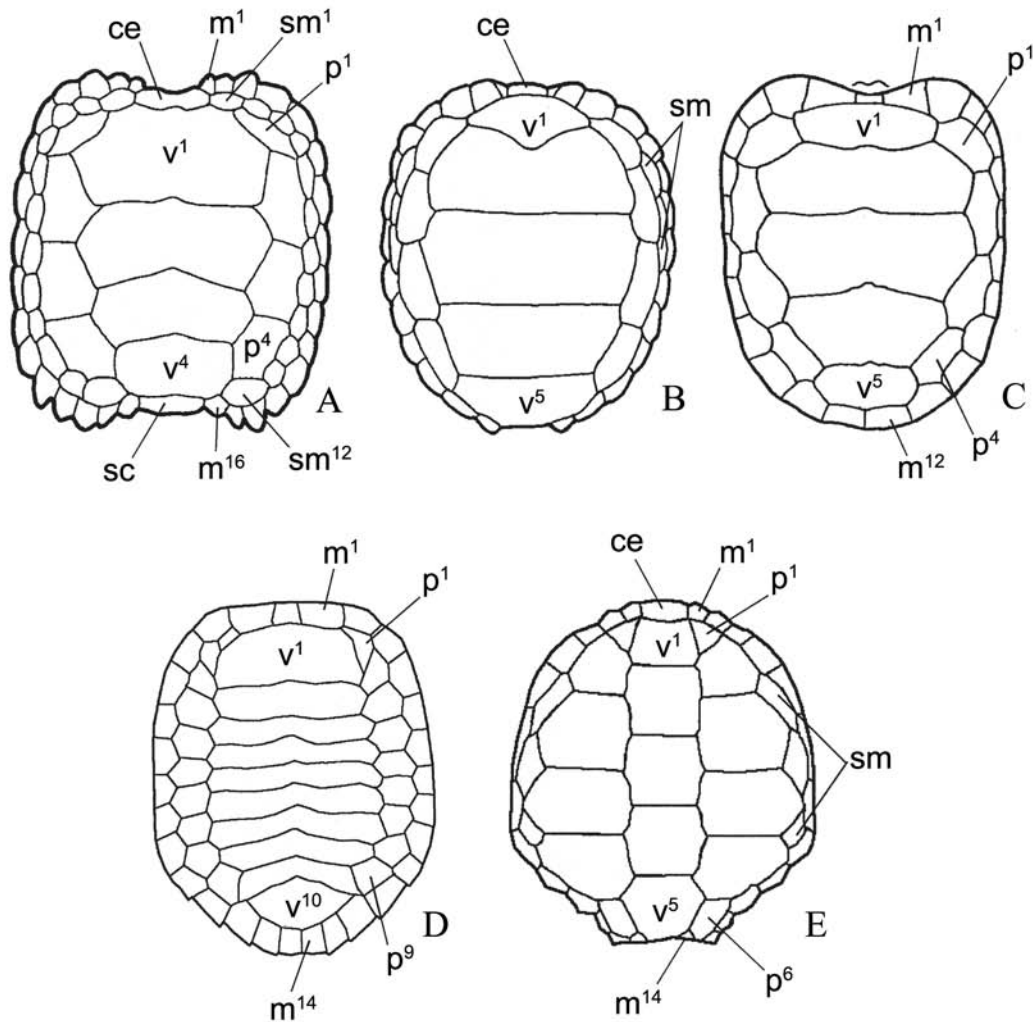
Fig. 5. Variants of the carapace scalation in different fossil turtles: A – *Proganochelys*; B – *Proterochersis*; C – *Kayentachelys*; D – *Sakya*; E – *Boremys* (A, B, C – from Gaffney, 1990; D – from Chkhikvadze, 1968; E – from Brinkman and Nicholls, 1991). Abbreviations are on Fig. 1.

additional scales appear, particularly in areas of 'vacant' myosepta. This process leads to the secondary polymerization of the shell mosaic and, as a rule, represents an anomaly in development (Newman, 1905; Cherepanov, 1987) that rarely stabilizes in the phylogenesis. Among recent forms, the polymeric state of pholidosis is demonstrated by sea turtles of the genus *Lepidochelys*, which have 13 pair of marginal scales and up to seven pairs of pleurals (Deraniyagala, 1939). However, the maxi-

mal number of horny elements are observed in the Pliocene geoemydid *Sakya* (Fig. 5D), which normally have up to ten vertebral and ten pairs of pleural scales (Chkhikvadze, 1968). The process of the secondary polymerization is likely demonstrated by the turtles of the family Baenidae (Gaffney, 1972; Brinkman and Nicholls, 1991). Some representatives of this group (*Boremys* and others), besides retaining ancestral features of pholidosis (e.g., a complete row of inframarginals), are char-

acterized by increasing the number of marginals (up to 14), and sometimes by the presence of additional anterior and/or posterior pairs of the scales in the pleural row (Fig. 5E). Based on morphogenetic data, the increased number of marginals indicates that the carapace of the Baenidae is formed by more segments than in other turtles.

The polymeric state of the pholidosis in turtles may also be a result of the division of the composite scales. Naturally, this process is restricted to the supracaudal and vertebral scales, which develop from paired anlage.

An absence of paleontological data is one reason why the state of pholidosis in the ancestors of turtles is suggested only hypothetically. However, these hypotheses are valid with respect to the number of longitudinal scale rows. In recent and fossil turtles, the maximum number of longitude rows is restricted to seven pairs. In the carapace, these are the vertebral (paired only in abnormal condition), pleural, supramarginal, and marginal rows. In the plastron, these are the inframarginal, plastral, and interplastral rows. Hypotheses attempting to explain a higher number of longitudinal scale rows in the direct ancestors of turtles are contentious, as they are based on indirect evidence (e.g., the pattern of tail pholidosis in *Chelydra*; Newman, 1905). The maximum number of scales in all mentioned longitude rows is known in the oldest turtles – Late Triassic *Proganochelys* and *Proterochersis*. Based on characters of pholidosis and some peculiarities of the bony shell, these turtles are referred to as 'amphichelydians' – the lowest grade of the chelonian organization (Zangerl, 1969).

Authors who have studied individual variability in the pholidosis of turtles have considered anomalies as recapitulations of the primitive state. However, schemes of the evolution of the shell scalation based on this consideration (Gadow, 1899, 1901; Newman, 1905; Deraniyagala, 1934; Grant, 1937a) were vulnerable to criticism. Among their arguments, these authors often use such terms as

«displacement,» «driving away,» and «compression» of one scale by others.

However, such processes are not observed during ontogeny. Moreover, the strict connection of the scale anlages with corresponding trunk segmentation excludes the possibility of their displacement in longitudinal direction. The displacement of the scale in transverse direction is restricted by rows of adjacent ones. Thus, it might be concluded that epidermal shell transformation in turtle evolution is associated with such morphogenetic processes as scale reductions, fusions, and only in rare cases, the appearance of novel horny elements. More specifically, the establishment and development of shell pholidosis in turtles is expressed in the following processes:

1. The fusion of left and right vertebral scales with formation of the unpaired (median) row. The unpaired row of scales in the vertebral area of the carapace is an ancient evolutionary acquisition of turtles. In the normal condition, such a state of pholidosis is typical for all turtles, both recent and fossil. The hypothesis about the primary pairs of the vertebral scales (Gadow, 1899) is based mainly on morphogenetic data. Besides that, the double row of asymmetrically-situated vertebral scales occurs sporadically in most recent forms (Zangerl and Johnson, 1957).

2. The correlated reduction of even and odd scales, which belong to vertebral and pleural rows respectively. This led to their position over segments, as well as the strict alternation (in staggered order) of the vertebral and pleural scales. Ideas about the stage-by-stage formation of scale order as a result of numerous reductions and displacements of scales (Newman, 1905) do not stand up to criticism from the morphogenetic positions.

In most turtles the number of vertebral (5) and pleural (4 pairs) scales is stable. However, *Proganochelys* has only four vertebral scales. This state is considered unique and suggests that *Proganochelys* represents a divergent branch in turtle evolution (Gaffney, 1990). The hypothesis

of Chkhikvadze (2003a), that the anterior vertebral scale of *Proganochelys* actually represents the fused first and second scales of the vertebral row, and that the first pair of the supramarginal scales represents additional pair of pleural scales, is not supported by any data.

The polymeric condition of pholidosis in the vertebral area is demonstrated by the recent geoemydid turtle *Notochelys platynota*. All specimens of this species typically have six vertebral scales (an additional small horny element is situated between vertebral scales IV and V). It should be noted that in other turtles, this variant usually is observed as an anomaly (Cherepanov, 1987). In primitive taxa, scales of the vertebral row are very wide and cover most of the carapace. Meanwhile, the scales of the pleural row are narrow and «displaced» towards the periphery of the carapace. During evolution, there is a clear tendency towards the narrowing of the vertebral scales and simultaneous widening of the pleural ones. This tendency reaches its maximum in representatives of the Emydidae, Geoemydidae, Kinosternidae, and Testudinidae. In the ontogenesis of *Emys* and *Testudo,* the recapitulation of this process is observed.

3. The reduction of the scales of the supramarginal row. The supramarginal scales are present in normal condition only in some turtles of the amphichelydian or mesochelydian grades. In *Proganochelys,* they form complete rows, consisting of 11–12 elements. In *Platychelys* and *Proterochersis* their number is diminished to three pairs. However, the latter genus exhibits a peculiar morphology of the posterior scales of the carapace (especially the marginals), which may indicate that they are in fact supramarginals reaching the edge of the carapace (Gaffney, 1990). Thus, the number of the scales under discussion in *Proterochersis* may reach seven or eight pairs (Fig. 5B). Among relatively derived turtles, the scales of supramarginal row are present in representatives of the Baenidae, for instance in *Boremys* (Fig. 5E). However in *Boremys*, the supramarginals

are distinguished by their large size (each supramarginal lies opposite to two marginals), which may suggest a secondary origin. This is also indicated by the fact that in *Kayentachelys* (Fig. 5C), a turtle that is closely related to basal cryptodirans (including Baenidae), supramarginals are absent (Gaffney et al., 1987).

4. The reduction of scales of the inframarginal row. In basal turtles (e.g., *Proterochersis, Kayentachelys,* Pleurosternidae, Baenidae and others) the inframarginal scales form a complete (uninterrupted) row consisting of 4–5 elements, which separate the marginals from the plastral scales (Fig. 6B, C). In the course of evolution, the number of the inframarginals reduces, mainly due to the disappearance of internal elements of the row; the anterior and posterior elements (axillary and inguinal) are more stable. Only turtles with a hinge developed in the bridge area (e.g., *Terrapene* and *Cuora*) are missing inframarginals completely. A reduction of the inframarginal scales is correlated with the compensatory widening of the abdominal and pectoral scales leading to contact between these plastral elements and the marginal scales.

5. The reduction in the number of the scales of the plastral row. The greatest number of paired plastral scales (nine) is described for *Proterochersis*—other turtles have no more than seven pairs of the plastral scales in the normal condition. This series includes the most anterior scales, which usually are called 'intergulars'; we call these 'gulars' (after Hutchison and Bramble, 1981) because of their contribution to the interplastral row is in question (Gaffney, 1990; Cherepanov, 1991a). The renaming of the intergular scales to the gular, and the former gular to the extragular, is considered reasonable because, despite changes to ideas about the homology of these elements, it allows us to retain the traditional (priority) names of scales in testudinoid turtles. Such an opinion about the nomenclature of these scales has become widely adopted in the paleontological literature (e.g., Brinkman and Nicholls, 1991). In the Testudinidae, Emydidae,
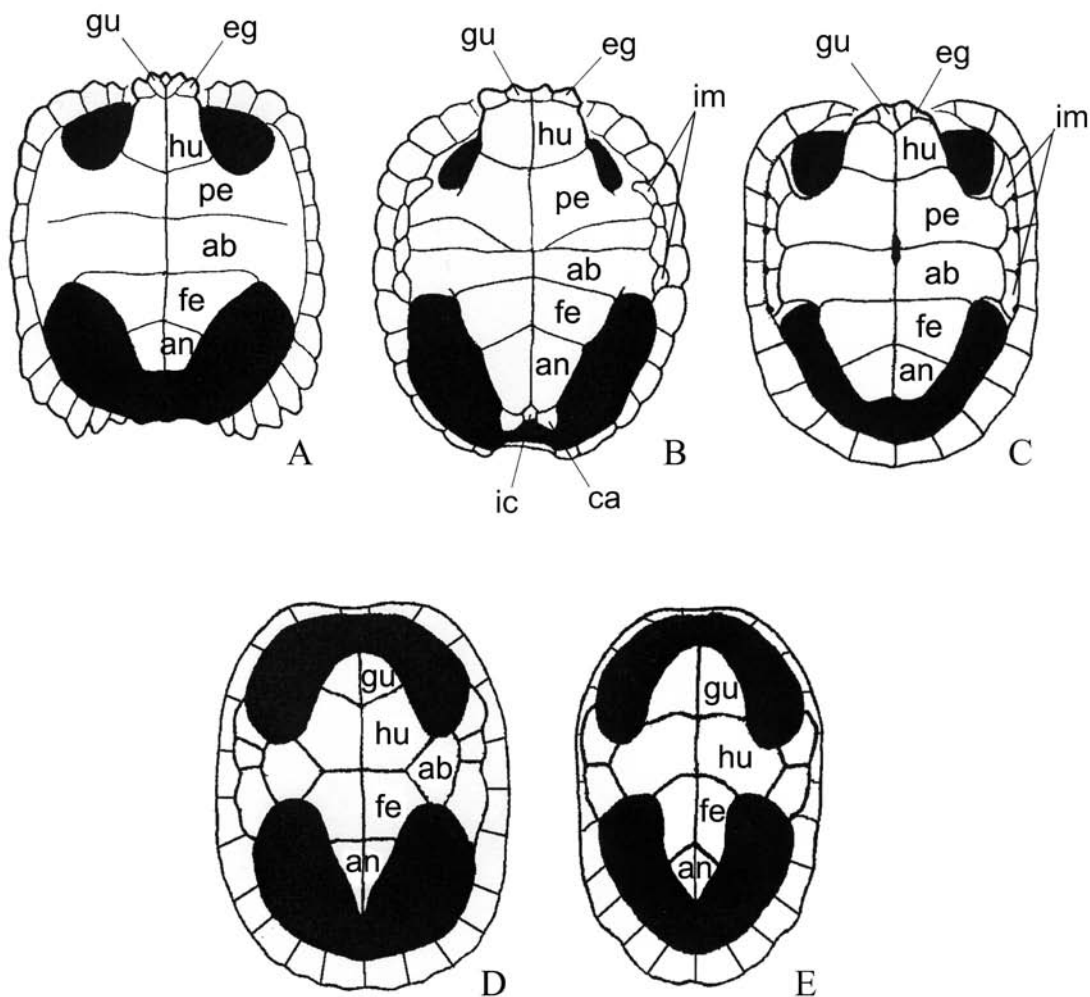
Fig. 6. Variants of the plastron scalation in different fossil and recent turtles: A – *Proganochelys*; B – *Proterochersis*; C – *Kayentachelys*; D – *Hoplochelys*; E – *Staurotypus* (A, B, C – from Gaffney, 1990; D, E – from Hutchison and Bramble, 1981). Abbreviations are on Fig. 1.

and related turtle families, the plastron bears only six pairs of scales. Based on paleontological data, these turtles are considered to have completely lost the extragular scales (Chkhikvadze, 1973). A stronger reduction of the plastral elements (extragular, pectoral, and abdominal) is demonstrated by representatives of the Dermatemydidae and Kinosternidae (Hutchison and Bramble, 1981). Thus, the process of reduction of the anterior and posterior (gular and caudal) and intermediate scales of the plastral row, for instance abdominals

in the line of kinosternids *Hoplochelys – Staurotypus* (Fig. 6c, d), took place in different turtle groups.

6. The fusion and reduction of the interplastral scales. The regular interplastral scales are present in basal turtles only. This series likely includes the unpaired scale between the gulars (i.e., the *intergulars* of Gaffney, 1990) in *Proganochelys* (Fig. 6A) and the intercaudal scale, which is positioned at the medial part of the xiphiplastra in *Proterochersis* (Fig. 6B). In recent turtles, the interplastral scales (postgular, sternal, and others) form at the joints

of horny sulci, separating the plastral scales, due to the meandering course of the sulci along the midline (Cherepanov, 1987). As a rule, these scales are unpaired and irregular. The fusion and reduction of the interplastral scales is likely caused by complete loss of segmentation along the midline of the abdomen of turtles after reaching the extremal dorsoventral flattening of the body.

It should be mentioned that the homologization of the scales in different turtles is rather difficult, and in some cases impossible. This is a reason for the numerous opinions about appropriate nomenclature for the epidermal scales in turtles, as discussed above. The difficulty of this question is due to an absence of clear criteria for distinguishing these scales. However, there are successful examples of the solution of this problem. It, although not indisputable (see Chkhikvadze, 2003b), is the work of Hutchison and Bramble (1981) on nomenclature of the plastral scales in two families of cryptodiran turtles, Dermatemydidae and Kinosternidae. These authors proposed that several criteria, such as the position and direction of growth of these scales, which allow one to ascertain primary patterns of transformation of pholidosis in the plastron, in the considered phylogenetic lines. Another achievement of this kind is the study of Pritchard (1984), which discuses the modification of the anterior carapace and plastral scales, in the evolution of the pleurodiran family Chelidae Gray, 1831.

The process of formation of the fundamental model of the shell pholidosis in the evolution of turtles (and their ancestors) was gradual and well regulated (Fig. 7). First, transformations appeared in the central parts of the carapace and plastron (areas of vertebral, pleural, and plastral scales), and later, the shell periphery. The primary cause for a change in the pattern of pholidosis towards a decreasing number of elements (from the primary polymeric condition) is the loss of the intertrunk mobility and the formation of the consolidated
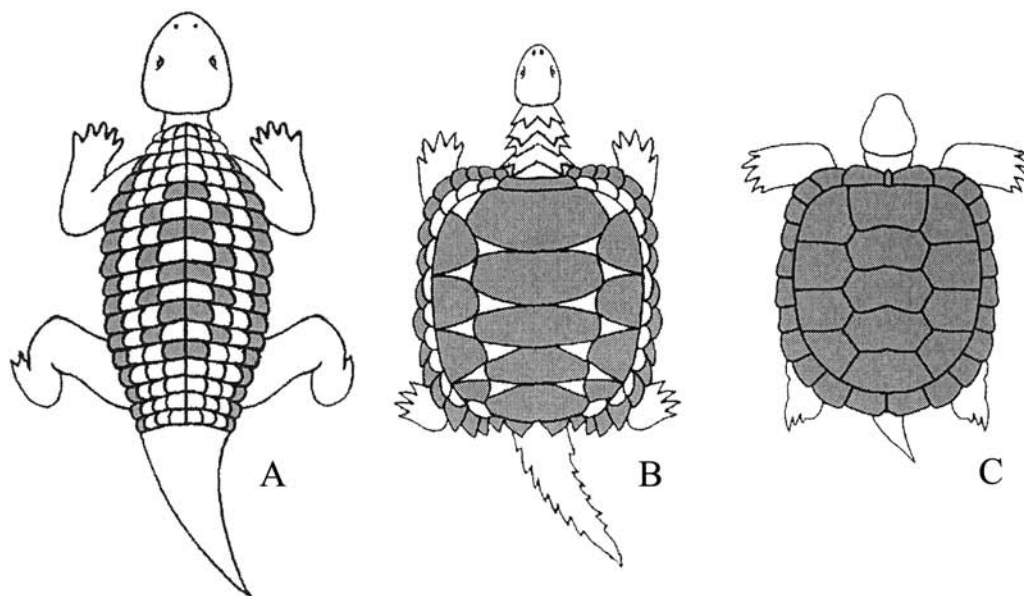
Fig. 7. Scheme of the evolutionary development of the carapace scalation: A – assumed primitive condition with the scales located in each trunk segment; B – plausible intermediate condition with the scales partially reduced; C – advanced condition with the established scale mosaic. Reducing scales are colorless.

bony shell. After formation of the fundamental shell model the evolutionary transformations of the epidermal mosaic were unessential, with rare exceptions. Therefore, we come to a conclusion that the main morphogenetic mechanisms of the pholidosis development (in particular, strict connection of areas of appearance of the scale anlages with the primary trunk segmentation and the correlated development of the pleural and vertebral scales, etc.) remained essentially unchanged to our time. This is a cause that in morphology turtles are one of the most stable groups among recent vertebrates.

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