Anomalies of the vertebral and pleural scutes in the Middle Jurassic turtle *Annemys variabilis* (Xinjiangchelyidae) from the Berezovsk coal mine (Krasnoyarsk Territory, Russia)

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Abstract

The anomalies of the vertebral and pleural scutes in the Middle Jurassic turtle *Annemys variabilis* (Xinjiangchelyidae) from the Berezovsk coal mine (Krasnoyarsk Territory, Russia) have been studied based of more than 1000 isolated neural plates. Symmetric and asymmetric abnormal scute patterns have been found. Comparison of the anomalies as well as their frequencies in *Annemys variabilis* and extant turtles demonstrates similar abnormal scute patterns. It is assumed that the high level of the scute variation of *Annemys variabilis* is caused by the instability of the developmental mechanisms, which are common for all turtles.

Keywords: Testudines, Xinjiangchelyidae, *Annemys variabilis,* Middle Jurassic, Krasnoyarsk Territory, scute abnormalities

Introduction

Turtles are characterized by a unique structure of the skin armor, having the bony shell covered by large epidermal horny scutes that are bordered by deep sulci. The latter are imprinted in the bone plates of the shell, making possible to study the scute patterns not only in the extant turtles, but also in the fossils, and allowing to apply these data in evolutionary studies (see Ascarrunz and Sánchez-Villagra, 2022).

The generalized pattern of the shell scutes in turtles is characterized by high evolutionary stability of the basal morphotype, recurring since the Triassic (Zangerl, 1969). At the same time, the individual variation of the scute pattern is wide, both by the number of the aberrant patterns and their frequency (Zangerl, 1969; Cherepanov, 2005, 2014). Thousands of abnormal turtle specimens belonging to many extant species have been described by now (Parker, 1901; Newman, 1906; Coker, 1910; Zangerl and Johnson, 1957; Ewert, 1979; Mast and Carr, 1989; Pritchard, 2007; Bujes and Verrastro, 2007; Cordero-Rivera, Ayres and Velo-Antón, 2008; Telemeco, Warner, Reida and Janzen, 2013; Cherepanov, 2014; Loehr, 2016; Cherepanov, Malashichev and Danilov, 2019; Brown and Davy, 2021; Cordero et al., 2022). Fossil taxa have been studied more poorly: there are only a few publications describing the variation of the shell elements, including the abnormalities of the horny shell, in extinct turtles (Brinkman and Nicholls, 1991; Joyce, Petričević, Lyson and Czaplewski, 2012; Püntener et al., 2014; Szczygielski, Slowiak and Dróżdż, 2018; Vlachos, 2020; Guerrero and Pérez-García, 2021). This is due to the lack of the mass material, without which the description of the variation is impossible.

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In this regard, the recently described *Annemys variabilis* Obraztsova, Krasnolutskii, Sukhanov, and Danilov, 2022 (Xinjiangchelyidae) from the Middle Jurassic of the Krasnoyarsk Territory (Siberia, Russia), represented by a huge number of the collected specimens including more than 2000 of isolated shell bones and several large shell fragments (Obraztsova et al., 2022), provides a unique opportunity for the study of variability in a fossil taxon. Among the carapace elements of this turtle, the neural plates demonstrate the greatest and most evident variation. A study of more than 1000 isolated neural plates of *Annemys variabilis* has shown that they are represented by several morphotypes that correspond to their position (ordinal number) in the neural series (Obraztsova, Shvets, and Danilov, 2020; Obraztsova, Krasnolutskii, Sukhanov, and Danilov, 2022). Many of these neural plates bear sulci, usually bilaterally symmetrical. However, asymmetric variants of the sulci were also found on some neural plates, which indicates the presence of the abnormal scute patterns in *Annemys variabilis*. The present work aims to describe these abnormal patterns.

Institutional abbreviations

ZIN PH, Paleoherpetological collection, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia. The term ‘Collection’ immediately preceding an institutional catalogue number (e.g., Collection ZIN PH 50) indicates that multiple specimens are accessioned under that number.

Material and methods

The studied material includes isolated neural plates and big shell fragments with preserved neural plates of *Annemys variabilis* from the collections ZIN PH 50, 187 and 290 (for other information on this material see Obraztsova, Krasnolutskii, Sukhanov, and Danilov, 2022). The total number of the studied isolated neural plates exceeds 1000; 499 of them have sulci. The only specimen of *Annemys variabilis* with the preserved entire neural series in articulation is ZIN PH 17/187 (Obraztsova, Krasnolutskii, Sukhanov, and Danilov, 2022: fig. 11).

The neural plates are the best preserved shell elements of *Annemys variabilis*. The neural plates are characterized by the relatively stable morphotypes correlating with their position in the neural series, which enables the position of an isolated plate in the series to be defined (Obraztsova, Shvets, and Danilov, 2020). The scute anomalies are best seen on the neural plates, since the neural plates are always affected by aberrations of the pattern of the vertebral scutes, which are the most frequent anomalies of the scute pattern in turtles (see Cherepanov, 2014). The correlation between pleural and vertebral scutes, arising from the specific developmental mechanism (see Cherepanov, 2014; Cherepanov, Malashichev and Danilov, 2019), allows us to reconstruct some general patterns of scute anomalies in *Annemys variabilis*. The mass material available makes it possible to define the frequency of normal and abnormal neural plates (i.e., neurals with normal and abnormal position of intervertebral sulci) and, based on this, to assess the rate of scute anomalies in *Annemys variabilis*.

Results

The study of complete shells and their fragments with plates in natural articulation made it possible to reconstruct the structure of the shell (Obraztsova, Krasnolutskii, Sukhanov, and Danilov, 2022).

Neural plates are represented by numerous complete specimens of several morphotypes, corresponding to neurals 1–8 (Fig. 1). In general, the anterior neurals are longer than wide, whereas the posterior ones are shorter, having almost equal length and width. Neurals 3–6 are hexagonal short-sided anteriorly, longer than wide concave anteriorly and convex posteriorly. Other neurals are variable in their shape. Neurals 1, 3, 5 (or 6) and 8 are always crossed by the intervertebral sulci, neurals 2, 4, and 7 are not crossed by the intervertebral sulci. All neurals have bone connection with the vertebrae, as they represent outgrowing perichondrial bones of the neural arches (Cherepanov, 1997).

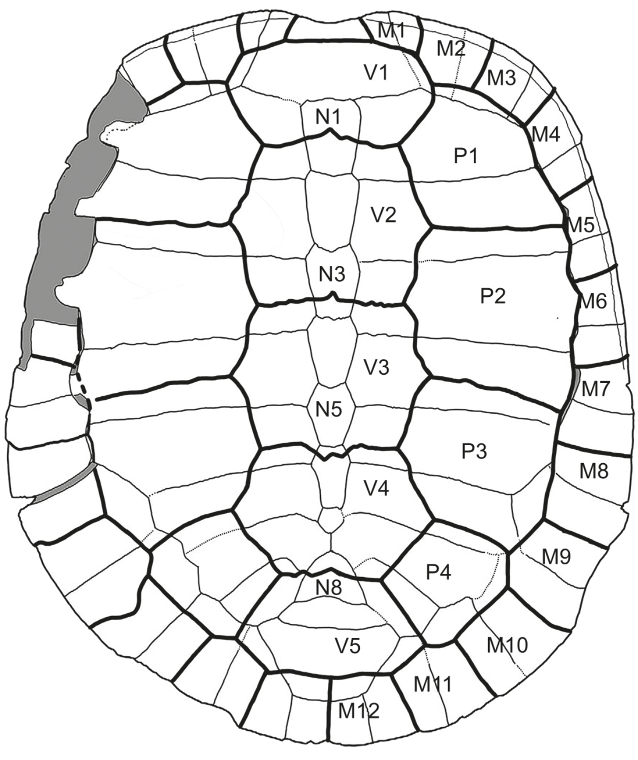

Fig. 1. Drawing of the shell of *Annemys variabilis* (ZIN PH 17/187) with the normal pattern of scutes and plates, dorsal view (from Obraztsova, Krasnolutskii, Sukhanov, and Danilov, 2022). Abbreviations: M — marginal scutes, N — neural plates, P — pleural scutes, V — vertebral scutes, 1–12 — serial numbers of plates and scutes.

Fig. 2. Dorsal view of the neurals of *Annemys variabilis* with the atypical position of the sulci. Numbers correspond to those in Table.

Table. Measurements (length, width and thickness) of the neurals of *Annemys variabilis* with the atypical position of the sulci. The numbers of the specimens correspond to those on Figure 2

ZIN PH No/290	Length	Width	Thickness	ZIN PH No/290	Length	Width	Thickness
1	16.36	12.57	3.44	33	17.37	12.81	3.73
2	15.0	11.16	3.62	34	16.62	12.9	3.39
3	8.54	6.4	2.22	35	15.33	10.53	3.33
4	11.23	8.27	2.0	36	14.72	9.14	2.9
5	19.11	10.95	4.52	37	11.21	10.57	3.71
6	17.4	16.86	5.9	38	13.38	9.09	3.71
7	22.67	15.81	6.73	39	15.74	10.73	3.64
8	17.52	12.62	6.55	40	13.11	10.44	2.86
9	18.54	12.83	6.62	41	11.45	9.92	4.2
10	16.27	10.73	4.81	42	12.12	10.01	2.68
11	15.06	12.84	4.88	43	10.82	7.29	2.34
12	15.77	13.27	2.51	44	10.04	9.38	2.03
13	17.86	12.57	2.77	45	17.89	13.65	5.62
14	16.21	11.38	4.05	46	14.74	11.65	3.63
15	12.97	8.55	2.02	47	17.87	15.66	5.07
16	13.16	11.05	2.46	48	16.37	13.74	4.84
17	11.34	8.23	2.8	49	16.83	14.57	3.84
18	10.6	9.21	3.47	50	15.68	11.81	5.36
19	10.1	8.51	2.0	51	16.78	11.11	3.2
20	7.51	7.36	1.85	52	12.73	9.52	2.77
21	17.54	17.18	5.21	53	14.17	9.83	3.0
22	28.98	22.7	4.6	54	17.79	15.68	5.18
23	13.88	14.25	7.16	55	12.6	8.66	2.39
24	21.07	14.27	4.17	56	9.24	7.33	2.58
25	18.57	14.5	4.92	57	15.45	11.31	3.66
26	19.17	14.58	3.85	58	14.21	9.76	3.59
27	21.08	11.31	3.1	59	13.2	9.34	3.62
28	18.32	14.0	4.21	60	14.29	8.84	2.26
29	4.29	11.4	4.26	61	13.58	9.51	2.76
30	19.06	13.84	3.67	62	13.0	9.29	2.67
31	11.96	7.87	1.64	63	12.86	9.45	3.17
32	15.0	11.03	3.2				

Neural 1 differs significantly from the other neurals with sulci. It is hexagonal short-sided posteriorly, rectangular, longer than wide. Its anterior border is convex, and the posterior one is concave or straight. The intervertebral sulcus crosses the plate in the middle part and forms a forward protrusion at the midline.

Neural 3 is crossed by the intervertebral sulcus in the posterior third of its length. The sulcus usually forms a forward protrusion at the midline.

Neural 5 is either crossed by the intervertebral sulcus (in shape of upturned V) near its posterior border, or not, as indicated by some neurals 6 crossed by the sulcus.

Neural 6 is relatively shorter than the previous neurals, and, if it is crossed by the intervertebral sulcus, the latter is located near its anterior border, and is usually V- or W-shaped.

Neural 8 is hexagonal or pentagonal, with a wide rectangular posterior part, and a triangle or trapezoid anterior part tapering anteriorly. The intervertebral sulcus crosses neural 8 in the middle part, forming an angle directed anteriorly at the midline.

The number of neurals with sulci is 499 (about 50 % neurals under study). Neurals with normal bilaterally symmetrically located sulci predominate, their number is 431. On 68 neurals (15.8 %) anomalies of the horny sulcus are observed (Fig. 2; Obraztsova, Krasnolutskii, Sukhanov, and Danilov, 2022, Fig. S2: M, N, X, Y, AA). The length of the abnormal neural plates ranges from 4.29 to 19.11 mm, width — from 6.4 to 16.86 mm, thickness — from 1.64 to 7.16 mm (Table). This indicates that they belong to different and numerous individuals of different ages.

All plates bearing abnormally located sulci have a typical hexagonal shape and retain a bilateral symmetrical shape. They correspond to neurals 3, 4, 5 and 6. Neurals 1 and 8 are absent among the anomalous plates.

Symmetrical anomalies were found only on five neural plates, which constituted 7.4 % of the total number of anomalous specimens. These anomalies are associated with the presence of an additional sulcus running along the medial line of the plate and dividing the area of the vertebral scute into two (left and right) parts. Thus, for some individuals of *Annemys variabilis* one can assume the presence of a paired row of symmetrically located vertebral scutes. On the neurals studied, the additional medial sulcus was found in two locations. On one of the plates, it crosses its posterior third, forming a T-shaped contact with the symmetrical intervertebral sulcus (Fig. 2: 1); on the other four neurals of this group, the medial groove is located in the anterior part of the plates (Fig. 2: 2–5). The medial groove on plate ZIN PH 4/290 has a special structure: it does not end in contact with the intervertebral sulcus, but continues caudally, obliquely crossing the entire plate (Fig. 2: 4). This indicates the presence not of one pair of vertebral scutes, as in other specimens of this group, but of at least two pairs.

A much more common deviation from the norm is the asymmetric location of the intervertebral sulcus. In our material, such asymmetries are observed in 63 neurals (92.6 % of anomalous specimens) and are represented by several variants: 1) the intervertebral sulcus crosses the neural plate along a wide arc, starting and ending at its anterior edge (Fig. 2: 6, 7); 2) the intervertebral sulcus crosses the neural plate at an angle with an S-shaped bend (Fig. 2: 8–21); 3) the intervertebral sulcus crosses the neural plate along an arc running from its lateral side to the upper (Fig. 2: 22–31) or lower edge (Fig. 2: 32); 4) the intervertebral sulcus crosses the neural plate at an angle in a relatively straight line (Fig. 2: 33–45); 5) the intervertebral sulcus has a V-shape and is asymmetrically located on the anterior edge of the neural plate (Fig. 2: 46–53); 6) the intervertebral sulcus is Λ-shaped and is asymmetrically located on the posterior edge of the neural plate (Fig. 2: 54–63). All of these variants indicate an asymmetrical shape of the vertebral scutes, and many of them suggest the presence of complex anomalies (see Discussion).

Discussion

Usually, the carapace scutes of turtles are organized in longitudinal rows (series) with strict bilateral symmetry. There are three scute series on the carapace: an unpaired vertebral (at the midline), paired pleural and paired marginal rows (see Fig. 1).

Numerous studies have shown a high frequency of scute anomalies among extant turtles (Coker, 1910; Cordero-Rivero, Ayres and Velo-Antón, 2008; Loehr, 2016; Brown and Davy, 2021, etc.). Anomalies of the scute pattern are represented by three main types (Cherepanov, 2014): 1) atypical shape or size of the scute(s); 2) the presence of additional (extraordinary) scute(s), and 3) the absence of some regular scute(s). These types of anomalies can be presented separately or combined in one specimen (Zangerl and Johnson, 1957; Pritchard, 2007; Cherepanov, 2014; Brown and Davy, 2021). Among anomalies of the horny pattern, asymmetric variants prevail. Aberrations of the horny shell can occur in all parts of the carapace, but the most variable area is the posteromedial part of the carapace (the area of the pleural and vertebral scutes). The most frequent aberration in this area is the presence of additional scutes (Zangerl and Johnson, 1957; Ewert, 1979; Mast and Carr, 1989; Bujes and Verrastro, 2007; Cordero-Rivero, Ayres and Velo-Antón, 2008; Cordero, 2022): they make up to 70 % of the total number of scute anomalies (Cherepanov, 2005).

The anomalies of the horny shell have been described only in a few fossil turtle taxa. Variation in the shape of vertebral scutes and the total number of scutes was reported for *Boremys pulchra* (Lambe, 1906) (Baenidae) from the Upper Cretaceous of Alberta (Brinkman and Nicholls, 1991). The presence of supernumerary pleurals in a single specimen of the fossil turtle *Tropidemys langii* Rütimeyer, 1873 (Plesiochelyidae) was interpreted as a developmental disorder (Püntener et al., 2014). Among Late Jurassic turtles, supernumerary pleurals are described in three specimens attributed to *Palaeomedusa testa* Meyer, 1860 (Joyce, 2003; Eurysternidae). Several patterns of the horny shell are described by almost complete shells of the extinct turtle *Echmatemys* Hay, 1906 (Geoemydidae) from the cen-

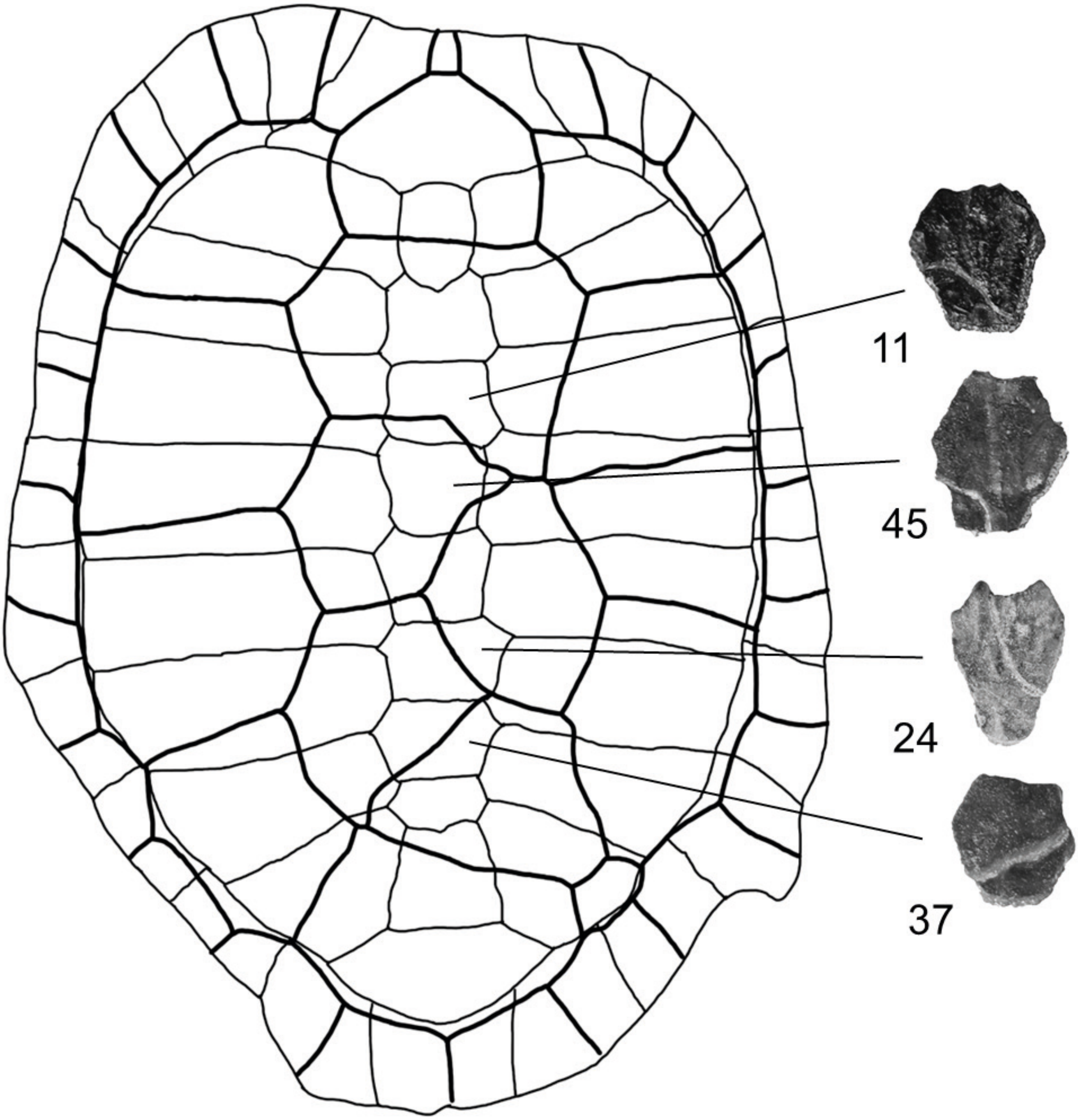

Fig. 3. Anomalous specimen of *Glyptemys insculpta* (LeConte, 1830) (= *Chelopus insculptus*; Emydidae; from Parker, 1901, modified drawing) with asymmetric variations in the position of the intervertebral sulci on the neural plates and some neurals of *Annemys variabilis* with a similar asymmetric position of the intervertebral sulcus. 11, 32, 24, 37 — numbers of the specimens, corresponding to those on Fig. 2.

tral United States. In particular, *Echmatemys callopyge* Hay, 1908 from the original slab of Gilmore is shown to have an additional asymmetric scute between the vertebral scutes 1 and 2 (Vlachos, 2020). Joyce et al. (Joyce, Petričević, Lyson and Czaplewski, 2012) redescribed the holotype of '*Terrapene longinsulae*' Hay, 1908 (current name *Terrapene ornata* Agassiz, 1857; Emydidae) from the Miocene/Pliocene Boundary (Latest Hemphillian) of Oklahoma having a complex zigzag anomaly with four pairs of asymmetric pleural scutes and two rows of eight asymmetric vertebral scutes. An article by Szczygielski et al. (Szczygielski, Slowiak and Dróżdż, 2018) is devoted to the shell variations in the stem turtles *Proterochersis* spp., describing the supernumerary scutes of the plastron and supernumerary abnormal scutes in the marginal series. A rare symmetrical anomaly was recently described in the carapace of one specimen of *Pleurosternon bullockii* (Owen, 1842) (Pleurosternidae) (Guerrero and Pérez-García, 2021). The presence of additional vertebral scutes affects at least the first three of the elements of this series and is manifested by a longitudinal split of each scute into two, forming a double row of symmetrical elements.

Thus, different variants of the scute anomalies are described in extinct turtles. The most common anomaly of the shell is the presence of additional scutes that are organized in several asymmetric and symmetrical patterns. In general, the anomalies of extinct taxa are similar to those described in living turtle species (see Cherepanov, 2014).

The anomalies found in the present study on *Annemys variabilis* fit into the general concept of variability of the turtle horny shell. A comparison of the abnormal arrangement of the sulci on the neurals of *Annemys variabilis* and abnormal specimens of extant turtles enables to reconstruct the abnormal scute patterns in *Annemys variabilis*. As in extant turtles, the most typical abnormal pattern is the presence of a double row of asymmetrically arranged vertebral scutes (Fig. 3). This is indicated by the neurals with a diagonal sulcus (Fig. 2: 6–45). They make up to 65 % of the total number of the aberrant neurals.

The presence of asymmetric vertebral scutes usually correlates with asymmetry of the pleural scutes (Zangerl, 1969; Ewert, 1979; Cherepanov, 2005, 2014; Moustakas-Verho et al., 2014; Zimm, Bentley, Wyneken and Moustakas-Verho, 2017; Brown and Davy, 2021). Such a complex abnormal pattern is called zig-zag (Pritchard, 2007). Apparently, in some cases it is also present in *Annemys variabilis*. A rarer abnormal pattern is a pair of symmetrically arranged vertebral scutes (see McKnight and Ligon, 2014: fig. 2). The presence of such an anomaly is indicated by the presence of an additional medial sulcus on the five neurals under study (see Fig. 2: 1–5). Another variant of aberrant variability is meandering of the intervertebral sulcus, leading to an asymmetrical position of its V- and Λ-shaped bend (Fig. 2: 46–63).

In modern natural populations of turtles, the frequency of an atypical arrangement of the scute mosaic can be very high, sometimes reaching up to 82 % (*Clemmys guttata* (Schneider, 1792); Emydidae; Brown and Davy, 2021). Such a high rate of anomalies is associated with a violation of the incubation processes. Natural and experimental studies have shown that temperature and humidity play an important role in the embryonic development of turtles, and their critical values cause morphogenesis disorders, including scute abnormalities (Lynn and Ullrich, 1950; Davy and Murphy, 2009; Telemeco, Warner, Reida and Janzen, 2013; Zimm, Bentley, Wyneken and Moustakas-Verho, 2017; Cordero et al., 2022). Another important factor of the anomalies in modern turtle populations is anthropogenic environmental pollution (Bishop et al., 1998; Ayres Fernández and Cordero Rivera, 2004). We believe that in the Middle Jurassic, the time of *Annemys variabilis*, the ecological situation was clean. Consequently, it could be assumed that the percentage of anomalies in this ancient turtle should be less than in modern taxa. However, this is not the case.

Based on the ratio of neurals with normal and abnormal scute arrangement, the rate of anomalies in the studied population of *Annemys variabilis* can be estimated within 15–20 %. This level is significantly lower than the maximum values of anomalies in a number of populations of modern turtles: 44 % in *Chersobius signatus* (Gmelin, 1789) (= *Homopus signatus*; Testudinidae; Loehr, 2016), 45 % in *Caretta caretta* (Linnaeus, 1758) (Cheloniidae; Coker, 1910), 69 % in *Emys orbicularis* (Linnaeus, 1758) (Emydidae; Cordero-Rivero, Ayres and Velo-Antón, 2008), 82 % in *Clemmys guttata* (Brown and Davy, 2021). But it is still higher, for example, than in terrapin populations, where the anomalies make from 2 to 11 % in *Chrysemys picta* (Schneider, 1783), *Deirochelys reticularia* (Latreille in Sonnini et Latreille, 1801) and *Trachemys dorbigni* (Duméril et Bibron, 1835) (Emydidae; Bujes and Verrastro, 2007; Davy and Murphy, 2009; McKnight and Ligon, 2014). Thus, we can assume that the scute anomalies in *Annemys variabilis* are caused by the basal mechanism of scute development in turtles.

Developmental studies of the living turtles have shown that scute primordia arise as localized epidermal placodes, and their location on the carapace is associated with somite segmentation of the embryo (Cherepanov, 2005, 2014; Moustakas-Verho et al., 2014; Moustakas-Verho and Cherepanov, 2015; Cherepanov, Malashichev and Danilov, 2019). Also, unlike the marginal placodes, the pleural and vertebral ones do not arise in each, but through one segment, thus keeping some of the segments vacant. Anomalies in turtle shell pholidosis derive mainly from the formation of the pleural and vertebral placodes in inappropriate segments of the body, which results in a change in the size, shape, or number of scutes. As a rule, the formation of additional pleural and vertebral scutes has an asymmetric character and a very high frequency of occurrence. The development of the vertebral scutes from paired primordia causes the appearance of such anomalies as a double row of symmetrical or asymmetric vertebral scutes.

The fundamental cause of the high frequency of anomalies of the scute mosaic in turtles is the presence of body segments vacant from the scute primordia. This determines the instability of the developmental mechanisms and the constant background nature of variability, manifested mainly in the asymmetric arrangement and the appearance of additional pleural and vertebral scutes. Since the presence of the scute anomalies is not critical for the survival of a turtle (Ewert, 1979; Sim, Booth, and Limpus, 2014; Cherepanov, 2014), the anomalies are not eliminated by the natural selection. The uniformity of anomalies in ancient and modern turtle taxa indicates the commonality of developmental processes of scute mosaic at all stages of turtle evolution.

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