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CARAPACE SCUTE VARIATIONS OF THE OLIVE RIDLEY SEA TURTLE (*Lepidochelys olivacea*): POLYMERIZATION AS AN EVOLUTIONARY TREND

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The carapace scute pattern is an important morphological feature of turtles that, along with the phylogenetic stability, has a high level of intraspecific variability. The olive ridley sea turtle (*Lepidochelys olivacea*; Cheloniidae) demonstrates extreme instability of pholidosis, and the aim of our study is to identify the range of the carapace scute variations in this species. We studied 655 *L. olivacea* hatchlings from nine natural clutches on the Southern coast of Sri Lanka and identified 120 different patterns of carapace scutes. The vertebral and pleural scutes were the most variable, ranging in number from four or five to ten. Five pairs of pleural scutes, a normal condition for some species of sea turtles, were found in only 11.9% of individuals. The hatchlings with six and seven scutes in the vertebral and pleural series were the most numerous. 13 pairs of marginal scutes were the stable norm in 92.7% of individuals. Newborn turtles with symmetrical scute patterns predominated (60.9%). Comparison of the pholidosis variability in hatchlings from different clutches revealed the presence of specific scute patterns. We assume that the clutch differences are more related to the genetic characteristics of the breeding turtles than to the influence of environmental factors. The unique variable pholidosis of *L. olivacea* demonstrates a trend toward scute polymerization, a rare phenomenon in turtle evolution.

Keywords: turtle carapace; scute variation; hatchling; Cheloniidae; *Lepidochelys olivacea*.

INTRODUCTION

The general plan of the pholidosis (scutation) arose in the early stages of turtle evolution and turned out to be stable for more than 200 million years (Gaffney, 1990; Ascarrunz and Sánchez-Villagra, 2022). This stability is connected with the conservatism of the genetic basis of the pholidosis, which determines the stability of the morphogenetic processes (Moustakas-Verho and Cherepanov, 2015). Although the general pattern of scutes has not undergone fundamental changes, some horny elements have been lost in the course of evolution. Thus, the oligomerization was the main evolutionary trend of the turtle pholidosis transformation (Zangerl, 1969; Ascarrunz and Sánchez-Villagra, 2022). Moreover, there is a reason to assume that the formation of the general pattern of scutes occurred due to the reduction of the primary polymeric scutes in the ancestors of turtles (Deraniyagala, 1934; Cherepanov, 2006, 2015).

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Numerous studies have shown that turtle shells are characterized by a very wide range of the intraspecific variability in the scute mosaic, especially in hard-shelled sea turtles, Cheloniidae (Gadow, 1899; Coker, 1910; Deraniyagala, 1939; Pritchard, 1969; Mast and Carr, 1989; Özdemir and Türkozan, 2006; Ergene et al., 2011; Sim et al., 2014; Kobayashi et al., 2017; Maffucci et al., 2020, Steenacker et al., 2023). Most researchers associate the appearance of scute anomalies with the direct influence of negative environmental factors during the incubation period (Lynn and Ullrich, 1950; Mast and Carr, 1989; Bujes and Verrastro, 2007; Telemeco et al., 2013; Zimm et al., 2017; Cortés-Gómez et al., 2018; Contreras-Merida and Morales-Mérida, 2021). In addition, it has been shown that anomalies may be related to the level of DNA methylation during embryonic development, which is an epigenetic mechanism associated with environmental conditions (Caracappa et al., 2016). However, it is assumed that some abnormalities may be genetic in nature (Zangerl, 1969; Cordero-Rivero et al., 2008; Velo-Antón et al., 2011; Kobayashi et al., 2017). Of particular interest in this connection is the extremely variable olive sea tur-

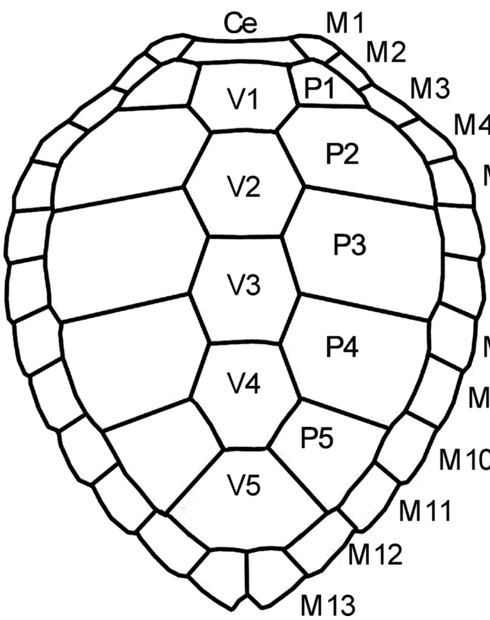

Fig. 1. The scheme of the general pattern of the horny shell in sea turtles (Cheloniidae) and nomenclature of carapace scutes. Abbreviations: Ce, cervical; M, marginals; P, pleurals; V, vertebrals; 1 – 13, serial numbers of scutes.

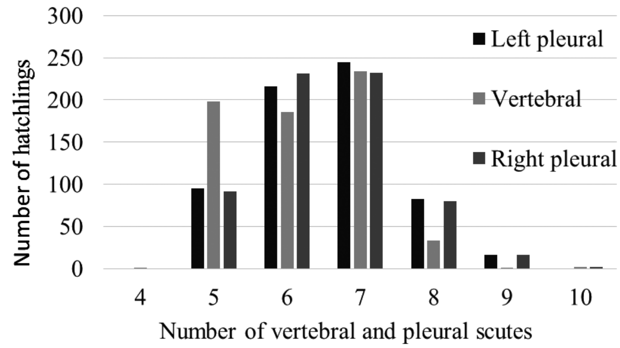

Fig. 2. The distribution of the number of vertebral, left and right pleural scutes in 655 hatchlings of *Lepidochelys olivacea*.

tle *Lepidochelys olivacea* (Eschscholtz, 1829). The horny shell of this turtle is so unstable that it is problematic to determine its normal state (Pritchard, 1969). In our opinion, the olive sea turtle is a good model species for identifying the natural range of variability in turtle shell scutes. Such a study seems important for understanding the evolutionary possibilities of transformation of the scute patterns in turtles in general and sea turtles in particular.

MATERIAL AND METHODS

We examined the carapace scute patterns of 655 *Lepidochelys olivacea* hatchlings from nine natural clutches. The study was conducted during two seasons (November – February 2015 and November – December 2016) on the Southern coast of Sri Lanka. Turtle eggs were obtained from natural nesting sites, and transferred to the territory of the turtle farm in the town of Kosgoda. The incubation site was located on a sandy beach 50 m from the water's edge. The eggs were incubated in sand 30 – 50 cm deep (30 – 40 eggs per nest with indication of the natural clutch number), at ambient temperature. Living newborn turtles were photographed in dorsal aspect and then released into nature. Photographing was performed using a Canon EOS 500D camera and Sigma AF 18 – 250 mm F3.5-6.3 HSM camera lens to get high resolution images. The photographs were viewed under high magnification to obtain a detailed description of the scute pattern. The data obtained were summarized in a table and statistically analyzed.

RESULTS

Variation in the scute series. The sea turtle modal scute pattern consists of one cervical, five vertebral, 4 – 5 pairs of pleural and 12 – 13 pairs of marginal scutes (Fig. 1). The majority of *L. olivacea* hatchlings (91.9%) had an unpaired cervical scute (Table). The presence of a pair of symmetrical or asymmetrical cervicals was found in 4.6% of individuals under study and 3.5% of individuals showed partial or complete fusion of the cervical scute with the vertebral scute 1.

The number of vertebral scutes varied from four to ten. Only one individual had nominally four vertebrals due to the partial fusion of the first two scutes of the vertebral series. The most common variants were those with five, six and seven vertebral scutes (30.2, 28.4, 35.8% of turtles). Only 5.6% of individuals had eight or more vertebrals. The increase in the number of scutes of the vertebral row occurred, first of all, due to the appearance of additional elements in the posterior half of the carapace. In the anterior part of the shell, additional vertebrals were rare (4.4%).

The number of pleural scutes varied from five to ten. Five pleurals, common in some sea turtles (*Lepidochelys kempii*, *Caretta caretta*), were observed in a relatively small number of *L. olivacea* studied (16.5%). Among them, symmetrical and asymmetrical structural variants were identified in a ratio of 4/1. Newborn turtles with six and seven pairs of pleurals were found with the same frequency — 21.1%, with eight pairs — 7%, with nine pairs — 1.2%. In general, an equal number of left and right pleurals were found in 409 hatchlings, which was 62.4% of the individuals studied.

The number of marginal scutes varied from ten to 15. The majority of hatchlings (92.7%) had 13 of their pairs (modal condition). Only seven hatched turtles (1.1%) demonstrated fewer than 13 marginals on one or both sides of the shell. The more frequent non-modal variants were the presence of one or a pair of additional marginal scutes in the caudal part of the carapace (6.25%).

Variation in the combination of vertebral and pleural scutes. The ratio of the number of vertebral and pleural scutes (V/P) showed a high level of variation (Fig. 2). In the studied turtles, we detected 24 combinations that differed in the number of vertebral and pleural scutes on the right or left side of the shell. Equal numbers of left and right pleurals were found in 17 combinations. Six combinations (7/5, 8/5, 8/6, 9/9, 9/10, and 10/10) were only asymmetrical. The combinations 5/5, 6/6, and 7/7 had the highest frequency of occurrence (12.8, 14.8, and 18.9%, respectively). In total, they were observed in 46.5% of the studied hatchlings.

Variation in patterns of scutes. Among the newborns of *L. olivacea*, 120 different patterns of carapace scutes were revealed (Appendix). The patterns are given as numeric formulas that reflect the number of scutes in the series (cervical-left marginal-left pleural-vertebral-right pleural-right marginal). The main contribution to the diversity of carapace pholidosis came from the vertebrals and pleurals, which demonstrate the greatest variability (Fig. 3). The number of asymmetric patterns predominated (86 variants or 71.7%). The frequency of manifestation of each was not great and did not exceed 4.1%. Symmetrical patterns were found in 399 turtles (60.9%) and were represented by 34 variants (28.3%). The most common were three patterns (1-13-5-5-5-13, 1-13-6-6-6-13, 1-13-7-7-7-13) found in 202 turtles (31%) in approximately equal proportions.

Variation of scutes in hatchlings from different clutches. We examined newborn turtles from nine clutches. Here we present data on six clutches. Other clutches were incomplete or mixed, and data on them is given in the appendix.

Hatchlings from clutch No. 1 (*n* = 86) had 24 scute patterns, of which the most common variant (24.4%) was 1-13-5-5-5-13. The number of vertebrals and pleurals varied in the range from five to seven, and only one individual had eight vertebrals. The proportion of turtles with an equal number of left and right pleurals was 65.1%.

Hatchlings from clutch No. 2 (*n* = 78) realized 36 scute patterns. The pattern of scutes that predominated in clutch No. 1 (see above) was absent, and the most common pattern was 1-13-6-6-6-13 (11.5%). The number of vertebrals and pleurals varied in the range from five to eight. The proportion of turtles with an equal number of left and right pleurals was 64.1%. More than 24% of individuals of the clutch had a specific anomaly — the fusion of the cervical scute and the vertebral scute 1.

Hatchlings from clutch No. 3 (*n* = 108) had the minimum number of patterns (17) among the studied clutches, and the most common variant was 1-13-6-5-6-13 (27.7%). The number of vertebrals and pleurals varied in the range from five to seven. The majority of turtles had five vertebrals (57.4%), while five pleurals are not typical for them (found in only 5.5% of clutch individuals). The proportion of turtles with an equal number of pleurals on both sides of the body was 68.5%, which slightly exceeded the average for all clutches (62.4%).

Hatchlings from clutch No. 4 (*n* = 103) had 20 patterns of pholidosis. The most common variant was 1-13-5-5-5-13 (39.7%). The number of vertebrals and pleurals varied from five to nine. The proportion of hatchlings with an equal number of right and left pleurals was 69.9%. This is the highest value among the studied clutches.

Hatchlings from clutch No. 5 (*n* = 123) realized the largest number of scute patterns (51). The common patterns were 1-13-5-5-5-13 (8.1%), 1-13-7-7-7-13 (12.2%), and 1-13-8-7-8-13 (8.1%). The number of vertebrals and pleurals varied from five to nine. An extremely increased number of these scutes (eight or nine) was found in 17.9% of turtles. The proportion of turtles with an equal number of left and right pleurals was 59.3%. A specific anomaly of pholidosis was an additional horny element between the cervical and the first vertebral scutes (13.8%).

Hatchlings from clutch No. 6 (*n* = 80) realized 48 patterns of pholidosis. The most common pattern was 1-13-7-7-7-13 (18.7%), other patterns were found mainly in single specimens. Vertebrals and pleurals varied in number in a wide range (from five to ten), but with a clear bias towards its increase (up to 8 – 10 in the series). The proportion of turtles with equal numbers of left and right pleurals was 56.2%, which is below the average level. This indicates a relatively high degree of their asymmetry. In addition, turtles from this clutch had several specific high-frequency anomalies such as the paired cervical scutes (15%), additional marginal scutes (21.2%), fusion of the first and the second vertebral scutes (12.5%), which were rare in turtles from other clutches.

DISCUSSION

The first description of the variability of scutes in newborns of *Lepidochelys olivacea* was given by Gadow (1899). Misclassifying them as juveniles of the loggerhead turtle *Caretta caretta* (see Pritchard, 2007), he found that these juveniles had significantly more cara-

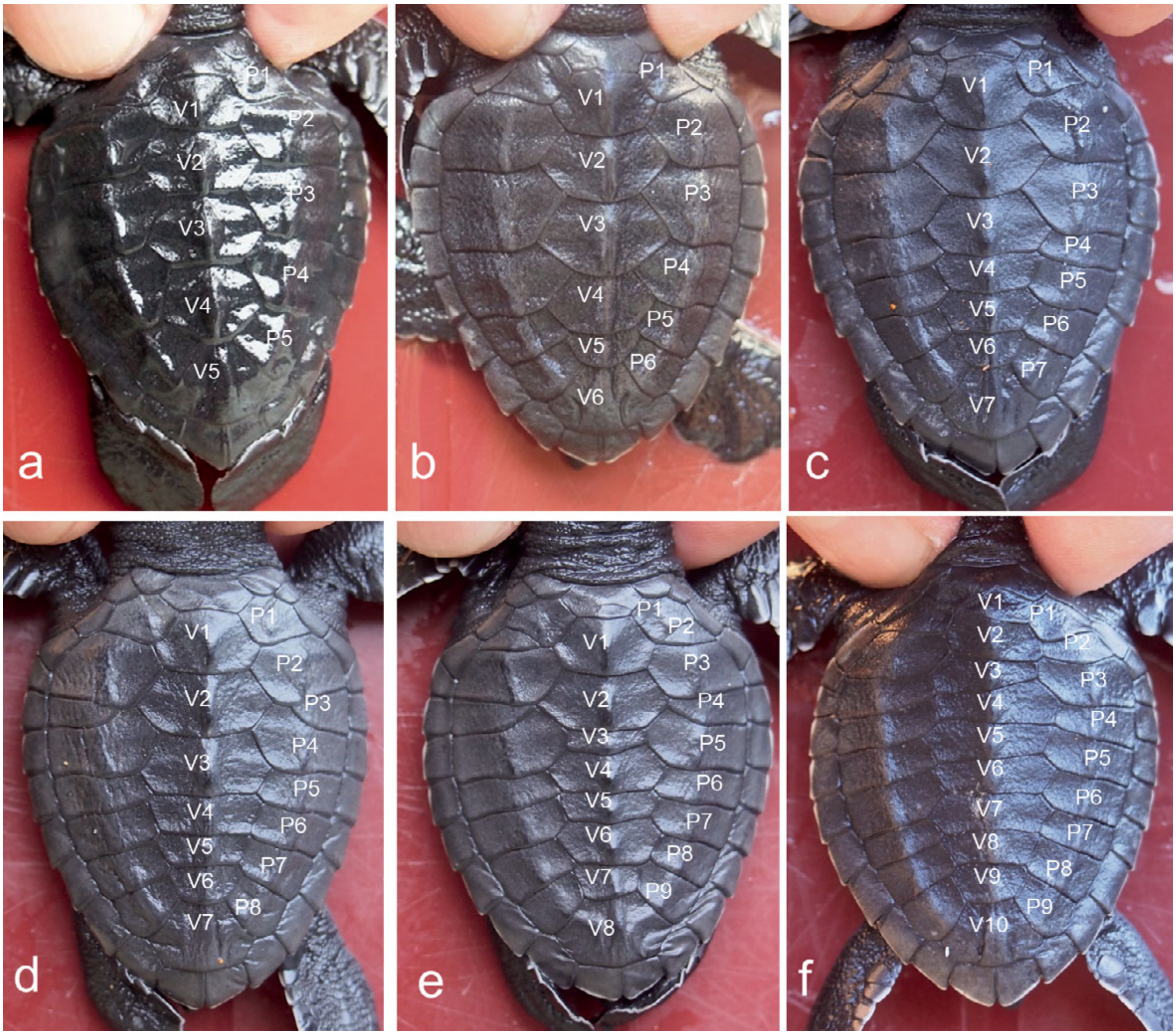

Fig. 3. *Lepidochelys olivacea* hatchlings with different symmetrical scute patterns in the carapace: (*a*) Specimen (P2104294) has five vertebrals and five pairs of pleurals, which are a modal pattern of the scutes of some sea turtles; (*b*) Specimen (P2124568) shows the pattern with six vertebral and six pairs of pleural scutes; (*c*) Specimen (P2175353) has seven vertebral and pleural scutes in each series; (*d*) Specimen (P2175459) has seven vertebral and eight pairs of pleural scutes; (*e*) Specimen (P2175587) has eight vertebral and nine pairs of pleural scutes; (*f*) Specimen (P2205926) shows the most polymeric number of scutes in the vertebral series (10) with nine pairs of pleural scutes. Abbreviations: P, pleurals; V, vertebrals; 1 – 13, serial numbers of scutes.

pace scutes than the loggerhead adults. The species diagnostic error led Gadow to the extravagant hypothesis that progressive reduction of scutes occurs during postnatal development, and the retention of polymeric anomalies in adults is the result of arrest of the development. In a phylogenetic sense, additional scutes were considered as atavisms (Newman, 1906), which became one of the reasons to assume the primary polymeric state of shell pholidosis in the ancestors of turtles (Deraniyagala, 1934; Grant, 1937; Zangerl and Johnson, 1957; Ewert, 1979).

Gadow's hypothesis was not confirmed by the subsequent study on the scute variability in newborns and adults of *C. caretta* (Coker, 1910), and later it was refuted by direct data on shell morphogenesis in turtles (Cherepanov, 1989, 2006; Moustakas-Verho and Cherepanov, 2015). These direct data shown that the pattern of scutes is formed during the embryonic stages of the development and does not change later. The location of the scute primordia (epidermal placodes) is determined by the primary somitic segmentation of the embryo, as they appear exclusively in the areas of the transverse trunk myosepta (septal zones). Since normally the pleural and vertebral scutes do not arise in each, but through one septal zone, some of them remain vacant. The presence of such vacant zones is the main cause for the variability of pholidosis and, in particular, determines the appearance of extraordinary scutes (Cherepanov, 2014).

As expected, in the *L. olivacea* hatchlings under study the scutes of the pleural and vertebral series were the most variable, their number varied from four to ten (Table 1). The most common individuals had six to seven vertebrals (64.2%), while five vertebral scutes that is a typical turtle norm observed in only 30.2% of the hatchlings. Five pleural scutes, modal for *Lepidochelys kempii* and *C. caretta* (Mast and Carr, 1989; Maffucci et al., 2020), were observed in a relatively small number of *L. olivacea* studied (16.5%). More than 70% of the hatchlings had six or seven pleural scutes on one or both sides of the body (Fig. 2). Additional scutes were present mainly in the posterior half of the carapace (91%). Symmetrical scute patterns with equal numbers of the left and right pleurals (Fig. 3) were found in 62.4% of the newborns. According to morphogenetic data (Cherepanov et al., 2019), the theoretical maximum number of vertebrals and pleurals in the shell of *L. olivacea* can reach 11 for a series, in case that the scute placodes occupy all potential septal zones. A close to the maximum number of vertebrals and pleurals (10 scutes) was found in three individuals, one of which had a symmetrical pattern (Fig. 3*f*). The number of marginal scutes varied from 10 to 15. The most of hatched turtles (92.7%) had 13 pairs of scutes, which can be considered a normal state.

Of 120 detected patterns of the scutes (Appendix), only 34 were symmetrical. Three of them (1-13-5-5-5-13, 1-13-6-6-6-13, 1-13-7-7-7-13; Fig. 3*a* – *c*) had a relatively high frequency, being found in 31% of turtles. The number of asymmetric patterns prevailed (86 variants, or 71.7%), but the frequency of each of them was not high. It has been suggested that scute asymmetries observed in turtle shells may indicate additional developmental anomalies and affect the survival of hatchlings (Telemeco et al., 2013). There is no doubt that this is true for extreme abnormal development leading to morphological deformity. But most scute anomalies apparently do not affect the life activity of juvenile and adult turtles (Bentley et al., 2020). In addition, symmetrical non-modal patterns can be considered as potential precursors of progressive evolution (Deraniyagala, 1934; Barry, 1935).

The presence of numerous scute patterns and the absence of a modal one indicates a unique arrangement of pholidosis in *L. olivacea*. However, in the population studied, we found several relatively high-frequency symmetrical states of the pholidosis with more carapace scutes than in other turtle taxa. Thus, the olive sea turtle's pholidosis shows an evolutionary tendency to polymerization of the scutes. This conclusion is supported by evidence from the fossil record. The oldest known *Lepidochelys* from the Upper Miocene of Panama had extraordinary six pairs of pleural scutes (Cadena et al., 2023). The authors of its description suggest that this extinct taxon

TABLE 1. Number of Carapace Scutes, Their Occurrence (*n*) and Frequency (%) in 655 Newborn *Lepidochelys olivacea*

Scute name	Scute number L/R	*n*	%
Nuchal	0	23	3.5
	1	602	91.9
	2	30	4.6
Vertebral	4	1	0.15
	5	198	30.2
	6	186	28.4
	7	234	35.8
	8	33	5.0
	9	1	0.15
	10	2	0.3
Pleural	5/5	79	12.1
	5/6	15	2.3
	5/7	1	0.15
	6/5	10	1.5
	6/6	138	21.1
	6/7	63	9.6
	6/8	5	0.75
	7/5	3	0.45
	7/6	78	11.9
	7/7	138	21.1
Marginal	7/8	25	3.8
	7/9	1	0.15
	8/6	4	0.6
	8/7	26	4.0
	8/8	46	7.0
	8/9	7	1.1
	9/7	2	0.3
	9/8	4	0.6
	9/9	8	1.2
	9/10	2	0.3
	10/12	1	0.15
	12/12	2	0.3
	12/13	1	0.15
	13/12	3	0.45
	13/13	607	92.7
	13/14	9	1.35
	14/13	13	2.0
	14/14	18	2.75
	15/14	1	0.15

Note. L, left; R, right.

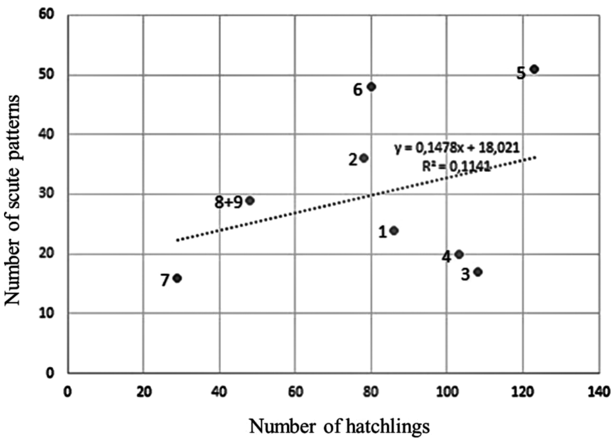

Fig. 4. The ratio of the number of scute patterns and the number of hatchlings in each of the clutches of *Lepidochelys olivacea*.

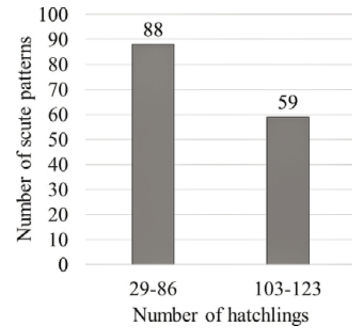

Fig. 5. The total ratio of the number of scute patterns in small (from 29 to 86 individuals per clutch, 321 individuals in total) and large (from 103 to 123 individuals per clutch, 334 individuals in total) clutches of *Lepidochelys olivacea*.

exhibits an intermediate scute pattern between the two extant taxa of the genus, *L. kempii* and *L. olivacea*.

Secondary polymerization of scutes as an evolutionary trend is characteristic not only of the genus *Lepidochelys*. *Caretta caretta* has an increased number of the pleural scutes to five pairs (Maffucci et al., 2020). A polymeric pholidosis pattern is observed in the geoemydid turtle *Notochelys platynota*, which normally has six vertebral scutes (Obst, 1986). However, the closest to theoretically possible number of scutes is probably observed in *Sakya riabinini* (Khosatzky, 1946; = *Sakya pontica* Bogachev, 1960), a fossil taxon of Geoemydidae, which normally had ten vertebrals and ten pairs of pleurals (see Danilov et al., 2017). Apparently, secondary polymerization also occurred in turtles of the family Baenidae, which were characterized by the increased number of marginals (up to 14) and frequently by the presence of supplementary pairs of the pleurals (Joyce and Lyson, 2017).

Lepidochelys olivacea has a wide geographical distribution in the Pacific, Indian and Atlantic Oceans. A study by Pritchard (1969) showed that different patterns of pholidosis predominated in different populations of the species: patterns with five pleurals were typical of the Gulf of Mexico population, patterns with six pleurals were typical of the population from Honduras, and patterns with seven or eight pleurals prevailed in the Suriname population. It is possible that these population differences are associated with genetic differences, perhaps with the influence of specific external factors. Thus, based on data from the incubation of *L. olivacea* eggs at a turtle farm in Santa Rosa, Guatemala, a direct effect of temperature on shell asymmetry was revealed (Contreras-Merida and Morales-Mérida, 2021). Another study found that the increase in scute asymmetry was proportional to the concentration of metals in turtle tissues due to environmental pollution (Cortés-Gómez et al., 2018). But probably not everything is determined by external factors. While studying the variability of turtle scutes, Zangerl (1969) identified so-called "repeating anomalies" that occurred with a certain frequency for a species (or genus) and were, in his opinion, a phenotypic manifestation of genotype variability. In addition, the percentage of abnormal turtles in different populations may be due to varying degrees of their resistance to unfavorable environmental factors, which, in turn, is associated with genetic differences in these populations (Cordero-Rivero et al., 2008; Velo-Anton et al., 2011). Thus, heritable factors cannot be excluded.

Comparison of *L. olivacea* hatchlings from different clutches shows that the number of patterns and their composition differ significantly (Appendix). There is no direct correlation between the number of patterns in a clutch and its size (Fig. 4). On the contrary, if we divide the clutches into small (29 – 86 individuals) and large (103 – 123 individuals) and summarize the data within these groups, it becomes obvious that small clutches are more diverse in the pholidosis than the large ones (Fig. 5). Thus, differences in the pholidosis appear not only at the population level (Pritchard, 1969), but also at the level of breeding individuals. Kobayashi et al. (2017) found that the frequency of anormal *Chelonia mydas* hatchlings was significantly higher in females with non-modal scute patterns compared to females with modal scute patterns; for these authors, scute abnormalities are heritable. Differentiation of the variability spectra of scutes in *L. olivacea* newborns from different clutches and the presence of specific anomalies for a number of clutches are apparently due to the genetic differences of their parents (see Glen et al., 2003) or their chemical status (see Cortés-Gómez et al., 2018), rather than to the influence of external factors, since all the clutches were incubated under similar conditions.

The olive sea turtle is characterized by an unstable scute arrangement with the trend towards polymerization. At the same time, symmetrical patterns of the pholidosis prevail over asymmetrical ones in a ratio of 2/1, which indicates the relative stability of the processes of embryonic development. Despite the absence of a single modal variant of the pholidosis, *L. olivacea* is characterized by a complex of three high-frequency symmetrical patterns with 5 – 7 scutes in the vertebral and pleural rows and 13 scutes in the marginal rows, which are found in 31% of the studied turtles. If we consider these pholidosis patterns to be a complex norm, we can see that their percentage is not very different from the proportion of modal patterns observed in some populations of other sea turtles, such as 34.1% in *C. caretta* (Ergene et al., 2011). It is possible that the wide variation in scutes of *L. olivacea* may have evolutionary significance, as some non-modal scute patterns may reflect intraspecific genetic diversity (Zangerl, 1969; Velo-Antón et al., 2011; Kobayashi et al., 2017). As an ecological strategy, morphological diversity increases the ability of sea turtles to adapt and survive in an ever-changing environment.

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APPENDIX. Scute Patterns of the Carapace and Their Occurrence (*n*) and Frequency (%) in 655 Hatchlings of *Lepidochelys olivacea* from Nine Natural Clutches on Island of Sri Lanka

No.	Ce-LM-LP-V-RP-RM	Clutch 1, *n* (%)	Clutch 2, *n* (%)	Clutch 3, *n* (%)	Clutch 4, *n* (%)	Clutch 5, *n* (%)	Clutch 6, *n* (%)	Clutch 7, *n* (%)	Clutch 8 + 9, *n* (%)	*n* (%)
1	1-12-6-4-6-12						1 (1.25)			1 (0.15)
2	1-13-5-5-5-13	21 (24.4)		3 (2.8)	41 (39.7)	10 (8.1)	3 (3.75)			78 (11.9)
3	1-10-5-5-6-12						1 (1.25)			1 (0.15)
4	1-13-5-5-6-13	4 (4.7)			1 (1.0)					5 (0.75)
5	1-13-6-5-5-13			3 (2.8)		1 (0.8)			1 (2.1)	5 (0.75)
6	0-13-6-5-6-13		2 (2.55)							2 (0.3)
7	1-13-6-5-6-13	3 (3.5)	8 (10.2)	30 (27.7)		2 (1.6)			4 (8.3)	47 (7.2)
8	1-14-6-5-6-13			1 (0.9)						1 (0.15)
9	2-13-7-5-5-13					1 (0.8)				1 (0.15)
10	1-13-6-5-7-13		1 (1.3)	2 (1.8)	1 (1.0)	1 (0.8)			1 (2.1)	6 (0.9)
11	1-13-7-5-6-13	1 (1.15)	2 (2.55)	6 (5.6)		4 (3.2)		1 (3.45)	1 (2.1)	15 (2.3)
12	1-13-6-5-8-13					1 (0.8)				1 (0.15)
13	0-13-7-5-7-13		1 (1.3)							1 (0.15)

No.	Ce-LM-LP-V-RP-RM	Clutch 1, *n* (%)	Clutch 2, *n* (%)	Clutch 3, *n* (%)	Clutch 4, *n* (%)	Clutch 5, *n* (%)	Clutch 6, *n* (%)	Clutch 7, *n* (%)	Clutch 8 + 9, *n* (%)	*n* (%)
14	1-13-7-5-7-13		2 (2.55)	14 (13.0)		3 (2.4)			3 (6.25)	22 (3.4)
15	1-13-7-5-8-13			3 (2.8)		1 (0.8)			1 (2.1)	5 (0.75)
16	1-13-8-5-7-13		1 (1.3)			1 (0.8)				2 (0.3)
17	1-13-8-5-8-13		2 (2.55)			1 (0.8)			3 (6.25)	6 (0.9)
18	1-13-5-6-5-13	1 (1.15)								1 (0.15)
19	1-13-5-6-6-13	4 (4.7)	1 (1.3)			2 (1.6)				7 (1.0)
20	1-13-6-6-5-13	1 (1.15)							1 (2.1)	2 (0.3)
21	1-13-7-6-5-13	1 (1.15)								1 (0.15)
22	1-13-6-6-6-12	1 (1.15)								1 (0.15)
23	1-13-6-6-6-13	12 (14.0)	9 (11.5)	14 (13.0)	9 (8.7)	3 (2.4)	4 (5.0)	1 (3.45)	4 (8.3)	56 (8.5)
24	2-13-6-6-6-13								1 (2.1)	1 (0.15)
25	1-14-6-6-6-13	1 (1.15)	1 (1.3)							2 (0.3)
26	0-13-6-6-7-13		1 (1.3)							1 (0.15)
27	1-13-6-6-7-13	1 (1.15)	5 (6.4)	9 (8.3)	3 (2.9)	4 (3.2)	1 (1.25)	1 (3.45)	3 (6.25)	27 (4.1)
28	1-14-6-6-7-13				1 (1.0)					1 (0.15)
29	0-13-7-6-6-13		1 (1.3)		1 (1.0)	2 (1.6)				4 (0.6)
30	1-13-7-6-6-13	2 (2.3)	2 (2.55)	7 (6.5)	5 (4.8)	3 (2.4)	2 (2.5)	3 (10.35)		24 (3.7)
31	1-14-7-6-6-14						1 (1.25)			1 (0.15)
32	0-13-7-6-7-13		4 (5.1)							4 (0.6)
33	1-13-7-6-7-13		5 (6.4)	6 (5.6)	3 (2.9)	6 (4.9)	1 (1.25)		2 (4.2)	23 (3.5)
34	2-13-7-6-7-13						1 (1.25)	1 (3.45)		2 (0.3)
35	1-13-7-6-7-14					1 (0.8)				1 (0.15)
36	0-13-6-6-8-13		2 (2.55)							2 (0.3)
37	0-13-8-6-6-13		1 (1.3)							1 (0.15)
38	1-13-7-6-8-13		1 (1.3)			2 (1.6)			1 (2.1)	4 (0.6)
39	1-13-8-6-7-13			1 (0.9)		1 (0.8)			1 (2.1)	3 (0.45)
40	2-14-8-6-7-13								1 (2.1)	1 (0.15)
41	1-13-8-6-8-13		1 (1.3)			6 (4.9)			2 (4.2)	9 (1.35)
42	1-13-8-6-9-13								1 (2.1)	1 (0.15)
43	1-14-8-6-9-13								1 (2.1)	1 (0.15)
44	1-13-9-6-7-13				1 (1.0)		1 (1.25)			2 (0.3)
45	1-13-9-6-8-13					1 (0.8)				1 (0.15)
46	1-13-9-6-9-13					1 (0.8)				1 (0.15)
47	2-13-9-6-9-13					1 (0.8)				1 (0.15)
48	1-13-5-7-6-13	1 (1.15)								1 (0.15)
49	1-13-5-7-6-14	1 (1.15)								1 (0.15)
50	1-13-6-7-5-13	1 (1.15)								1 (0.15)
51	1-13-5-7-7-13	1 (1.15)								1 (0.15)
52	1-14-7-7-5-14						1 (1.25)			1 (0.15)
53	0-13-6-7-6-13		1 (1.3)							1 (0.15)
54	1-13-6-7-6-13	11 (12.8)	1 (1.3)	3 (2.8)	1 (1.0)		7 (8.75)			23 (3.5)
55	2-13-6-7-6-13	1 (1.15)								1 (0.15)
56	1-13-6-7-6-14	1 (1.15)								1 (0.15)
57	1-14-6-7-6-13						1 (1.25)			1 (0.15)
58	1-13-6-7-7-13	5 (5.8)	2 (2.55)	1 (0.9)	6 (5.8)	3 (2.4)	1 (1.25)	5 (17.2)		23 (3.5)
59	2-13-6-7-7-13		1 (1.3)					2 (6.9)		3 (0.45)
60	1-14-6-7-7-14						1 (1.25)			1 (0.15)
61	1-13-7-7-6-13	7 (8.2)	2 (2.55)	2 (1.8)	4 (3.9)	5 (4.1)	2 (2.5)	2 (6.9)	1 (2.1)	25 (3.8)
62	2-13-7-7-6-13						2 (2.5)			2 (0.3)
63	1-13-7-7-6-14					1 (0.8)				1 (0.15)
64	1-14-7-7-6-14						1 (1.25)			1 (0.15)
65	1-13-6-7-8-13					1 (0.8)			1 (2.1)	2 (0.3)
66	1-13-8-7-6-13						1 (1.25)			1 (0.15)
67	2-13-8-7-6-13							1 (3.45)		1 (0.15)

No.	Ce-LM-LP-V-RP-RM	Clutch 1, *n* (%)	Clutch 2, *n* (%)	Clutch 3, *n* (%)	Clutch 4, *n* (%)	Clutch 5, *n* (%)	Clutch 6, *n* (%)	Clutch 7, *n* (%)	Clutch 8 + 9, *n* (%)	*n* (%)
68	2-14-8-7-6-14						1 (1.25)			1 (0.15)
69	0-13-7-7-7-13		1 (1.3)						2 (4.2)	3 (0.45)
70	0-14-7-7-7-13					1 (0.8)				1 (0.15)
71	1-12-7-7-7-12								1 (2.1)	1 (0.15)
72	1-12-7-7-7-13						1 (1.25)			1 (0.15)
73	1-13-7-7-7-12						1 (1.25)			1 (0.15)
74	1-13-7-7-7-13	3 (3.5)	8 (10.2)	3 (2.8)	18 (17.4)	15 (12.2)	15(18.75)	3 (10.35)	3 (6.25)	68 (10.4)
75	2-13-7-7-7-13						1 (1.25)	2 (6.9)		3 (0.45)
76	1-13-7-7-7-14		1 (1.3)							1 (0.15)
77	1-14-7-7-7-13					1 (0.8)	1 (1.25)			2 (0.3)
78	0-13-7-7-8-13				1 (1.0)					1 (0.15)
79	1-13-7-7-8-13				3 (2.9)	4 (3.2)		2 (6.9)	1 (2.1)	10 (1.5)
80	1-14-7-7-8-14		1 (1.3)							1 (0.15)
81	0-13-8-7-7-13		1 (1.3)		1 (1.0)					2 (0.3)
82	1-13-8-7-7-13		1 (1.3)		1 (1.0)	1 (0.8)	2 (2.5)		1 (2.1)	6 (0.9)
83	2-13-8-7-7-13							2 (6.9)		2 (0.3)
84	1-13-8-7-7-14					1 (0.8)				1 (0.15)
85	1-14-8-7-7-14						3 (3.75)			3 (0.45)
86	1-13-7-7-9-13					1 (0.8)				1 (0.15)
87	1-13-8-7-8-12						1 (1.25)			1 (0.15)
88	1-13-8-7-8-13		2 (2.55)			10 (8.1)		1 (3.45)	2 (4.2)	15 (2.3)
89	2-13-8-7-8-13					1 (0.8)	1 (1.25)			2 (0.3)
90	1-13-8-7-8-14					1 (0.8)				1 (0.15)
91	1-14-8-7-8-13					2 (1.6)				2 (0.3)
92	1-14-8-7-8-14					1 (0.8)				1 (0.15)
93	1-13-8-7-9-13					2 (1.6)	1 (1.25)			3 (0.45)
94	1-13-8-7-9-14					1 (0.8)				1 (0.15)
95	2-14-8-7-9-14						1 (1.25)			1 (0.15)
96	1-13-9-7-8-13					2 (1.6)				2 (0.3)
97	1-14-9-7-8-14						1 (1.25)			1 (0.15)
98	1-13-9-7-9-13					1 (0.8)			2 (4.2)	3 (0.45)
99	1-13-6-8-5-13						1 (1.25)			1 (0.15)
100	2-13-6-8-5-13						1 (1.25)			1 (0.15)
101	1-15-6-8-7-14						1 (1.25)			1 (0.15)
102	1-13-7-8-6-13		1 (1.3)				1 (1.25)			2 (0.3)
103	2-13-7-8-6-13						1 (1.25)			1 (0.15)
104	1-14-7-8-6-14						1 (1.25)	1 (3.45)		2 (0.3)
105	1-13-7-8-7-13					1 (0.8)	1 (1.25)			2 (0.3)
106	2-13-7-8-7-13					1 (0.8)				1 (0.15)
107	1-14-7-8-7-14	1 (1.15)								1 (0.15)
108	1-13-7-8-8-13				1 (1.0)		1 (1.25)			2 (0.3)
109	2-13-7-8-8-13					1 (0.8)				1 (0.15)
110	1-13-7-8-8-14						1 (1.25)			1 (0.15)
111	1-13-8-8-7-13		1 (1.3)		1 (1.0)	1 (0.8)				3 (0.45)
112	2-13-8-8-7-13						1 (1.25)	1 (3.45)		2 (0.3)
113	2-14-8-8-7-13						1 (1.25)			1 (0.15)
114	1-13-8-8-8-13		1 (1.3)			3 (2.4)	2 (2.5)		1 (2.1)	7 (1.0)
115	1-14-8-8-8-14						1 (1.25)			1 (0.15)
116	2-14-8-8-8-14						1 (1.25)			1 (0.15)
117	1-13-9-8-9-13					1 (0.8)			1 (2.1)	2 (0.3)
118	1-14-9-9-10-14					1 (0.8)				1 (0.15)
119	1-13-9-10-9-13						1 (1.25)			1 (0.15)
120	1-13-9-10-10-13						1 (1.25)			1 (0.15)
Total	86 (100)	78 (100)	108 (100)	103 (100)	123 (100)	80 (100)	29 (100)	48 (100)	655 (100)	

Note. Ce, cervicals; LM, left marginals; LP, left pleurals; V, vertebrals; RP, right pleurals; RM, right marginals.