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Shell Anomalies in the European Aquatic Stem Turtle *Pleurosternon bullockii* (Paracryptodira, Pleurosternidae)

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Abstract: The uppermost Jurassic to lowermost Cretaceous stem turtle *Pleurosternon bullockii* is the pleurosternid (Testudinata, Paracryptodira) known by the largest number of specimens worldwide, composing the largest European collection of Lower Cretaceous complete and partial shells for a turtle taxon. The availability of numerous specimens as well as their generally good preservation allowed for recent detailed characterization of the shell of this species, including states that are variable at the intraspecific level (individual variability, sexual dimorphism, and ontogenetic development). However, extreme cases of morphological variation corresponding to anomalies have not been addressed in detail, neither for *P. bullockii* nor for any other member of Paracryptodira. In this context, the study of several shell anomalies in *P. bullockii* is carried out here. Fourteen specimens showing anomalies are recognized and examined here to determine the frequency and distribution of these shell anatomical deviations. All these anomalies are described and figured. The morphogenetic cause of each of them is discussed. As a consequence, a relatively broad spectrum of anomalies is reported for *P. bullockii*. None of the anomalies seem to present negative consequences for vital activities of the specimens since none compromised the main functions of the shell.

Keywords: Testudinata; stem Testudines; pleurosternids; Mesozoic; United Kingdom; morphological deviations

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1. Introduction

Turtles are a highly specialized group of reptiles, characterized by the presence of a shell composed by osseous plates, generally covered by keratinous scutes. This mosaic of shell elements is subjected to a relatively high phylogenetic stability, but a significant degree of intraspecific variability can be recognized [1–5]. Thus, turtles show relatively high individual variability regarding the frequency of abnormal variants of the shell elements, generally corresponding to anatomical deviations originating during the embryonic development [3,4,6,7]. Shell anomalies of morphogenetic origin have been documented in turtles for more than a century, generally in extant taxa (e.g., [1,8–16]), but have also been documented for some extinct forms (e.g., [17–24]). The sample size available for most extinct species is relatively limited, and therefore, the probability of observing anomalous individuals in the study sample is low. Therefore, shell deviations for extinct taxa are commonly reported as isolated occurrences. In addition, most of the anomalies recognized in the fossil remains of turtles have been generally reported without providing any type of analysis on its morphogenetic cause or detailed descriptions. Consequently, the information and, therefore, knowledge about this type of variation in extinct taxa are relatively scarce.

In this context, a detailed study of numerous shell anomalies identified for the European extinct turtle *Pleurosternon bullockii* (Owen, 1842) [25] is carried out here. *Pleurosternon bullockii* corresponds to the best represented pleurosternid (Paracryptodira) so far known and the only aquatic stem turtle (i.e., a member of Testudinata not attributable to the crown Testudines) identified in both the Upper Jurassic (Tithonian) and the Lower Cretaceous

(Berriasian) records [26,27]. This study is based on the analysis of fourteen anomalous individuals of *P. bullockii* from the British record (i.e., from the Purbeck and Portland levels of Dorset), representing mature and juvenile stages. A relatively high intraspecific variability (i.e., polymorphisms, sexual dimorphism, and ontogeny) was recently documented for the shell of this taxon [26,27]. However, extreme cases of the morphological variability (i.e., abnormal variants) have not been considered so far. Thus, the aim of the present study is to record and describe the distribution and frequency of the occurrence of anomalies of the shell of the stem turtle *P. bullockii* and to evaluate the possible morphogenetic cause of each abnormality, providing, for the first time, detailed data on this type of intraspecific variation not only in Pleurosternidae but also in Paracryptodira.

2. Materials and Methods

A total sample of seventy-four specimens of *Pleurosternon bullockii*, corresponding to both complete shells as well as partial carapace and plastra (see [27] and the references therein), have been analyzed in order to identify the anomalous specimens. The number of anomalous specimens corresponds to thirteen mature individuals and one juvenile (Figures 1 and 2). All of these specimens come from the Berriasian (Lower Cretaceous) levels of the Purbeck Group (Isle of Purbeck, Dorset, UK), except for NHMUK OR 44807 (Figure 2D), which is from the Tithonian (Upper Jurassic) of the Portland Group (Isle of Portland, Dorset).

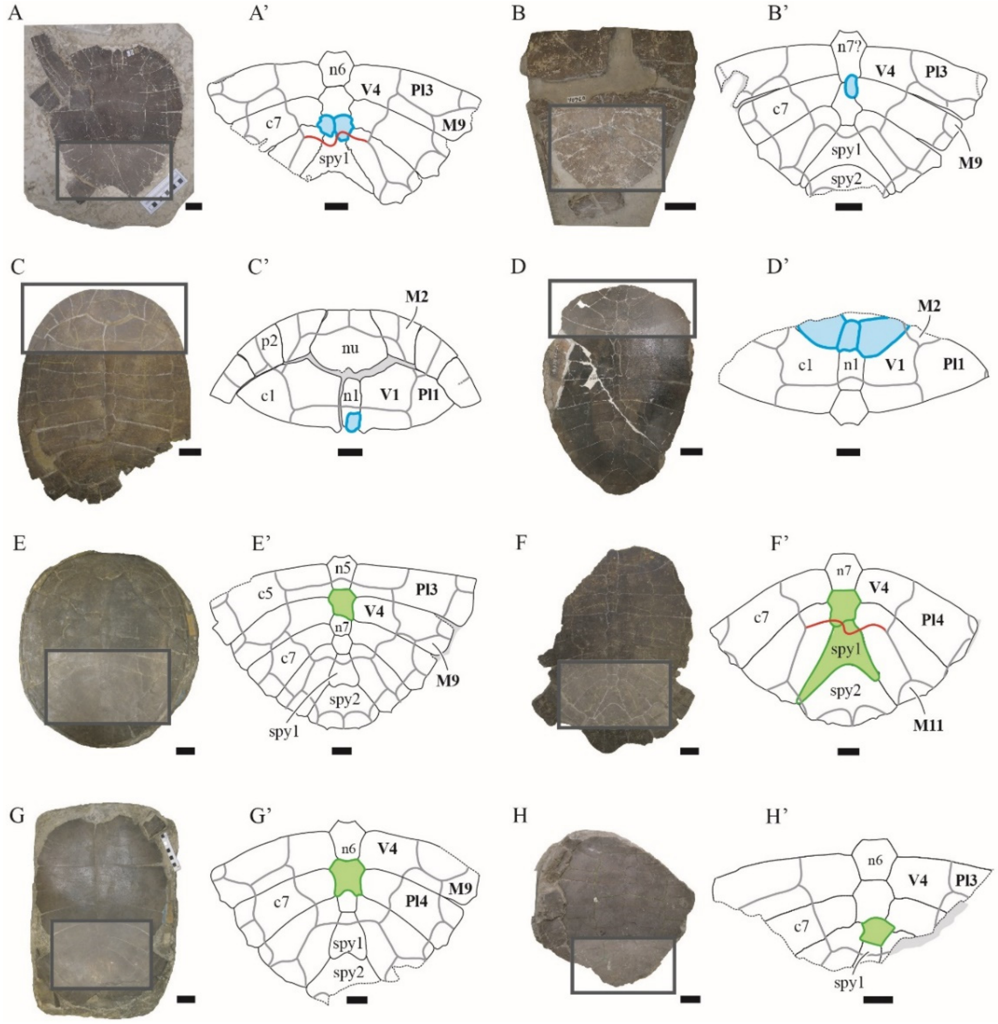

Figure 1. Anomalous carapaces of *Pleurosternon bullockii* (Paracryptodira, Pleurosternidae), from the Berriasian (Early Cretaceous) of Swanage (Dorset, UK). All of them are in dorsal view. (**A**,**A'**) OUMNH K54009, (**B**,**B'**) NHMUK OR 40960, (**C**,**C'**) NHMUK OR 43621, (**D**,**D'**) YPM VPPU 3364, (**E**,**E'**) CAMSM J5327, (**F**,**F'**) NHMUK OR 47401, (**G**,**G'**) CAMSM J5328,

and (**H**,**H′**) NHMUK R 6880. Blue corresponds to additional elements, green corresponds to the unusual shape of the plates, and red corresponds to the unusual shape of the scutes. Abbreviations for the plates (in lowercase and normal type): c, costal; n, neural; nu, nuchal; p, peripheral; and spy, suprapygal. Abbreviations for the scutes (in uppercase and in bold type): M, marginal; Pl, pleural; and V, vertebral. The scale bars in the photographs equal 4 cm, and those in the drawings equal 2 cm.

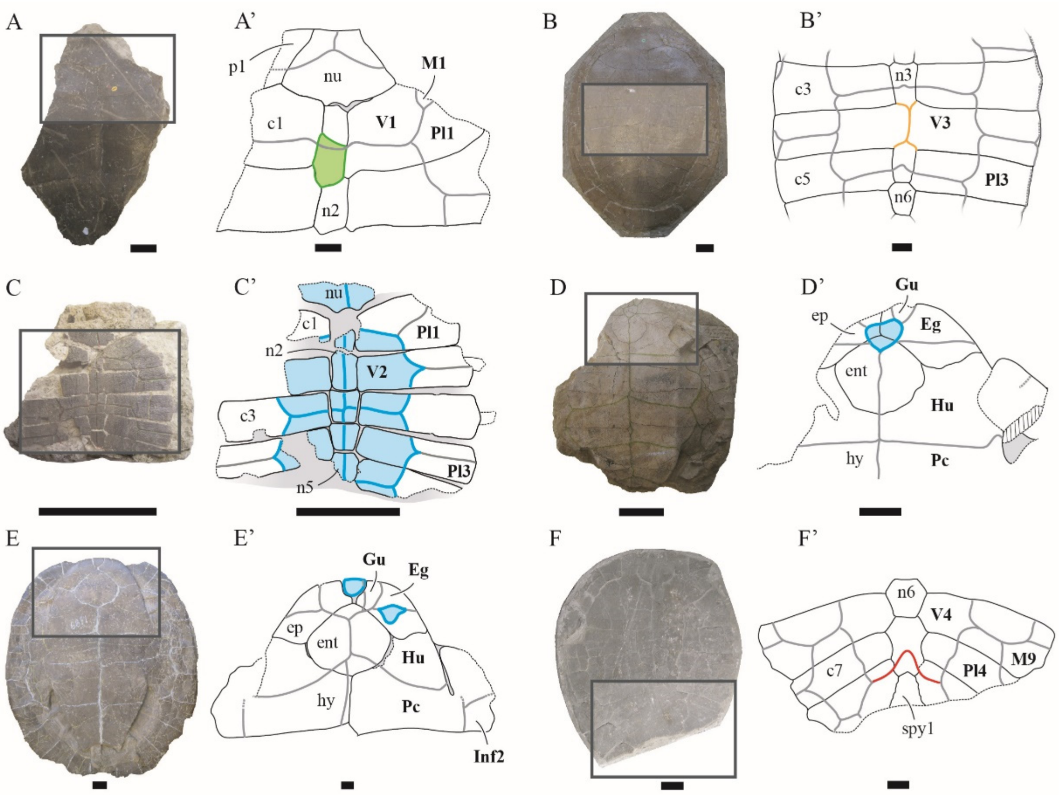

Figure 2. Anomalous shells of *Pleurosternon bullockii* (Paracryptodira, Pleurosternidae). All specimens are from the Berriasian (Early Cretaceous) of Swanage (Dorset, England), except NHMUK OR 44807, which is from the Tithonian (Late Jurassic) of the Isle of Portland (Dorset). (**A**,**A′**) NHMUK 24298 in dorsal view, (**B**,**B′**) NHMUK OR 28618 in dorsal view, (**C**,**C′**) NHMUK 48263c in dorsal view, (**D**,**D′**) NHMUK OR 44807 in ventral view, (**E**,**E′**) NHMUK R 1889 in ventral view, and (**F**,**F′**) DORCM G6262 in dorsal view. Blue corresponds to additional elements, green corresponds to the unusual shape of the plates, red corresponds to the unusual shape of the scutes, and orange corresponds to the absence of regular shell plates. Abbreviations for the plates (in lowercase and normal type): c, costal; ent, entoplastron; ep, epiplastron; hy, hyoplastron; n, neural; nu, nuchal; p, peripheral; and spy, suprapygal. Abbreviations for the scutes (in uppercase and in bold type): Eg, extragular; Gu, gular; Hu, humeral; Inf, inframarginal; M, marginal; Pc, pectoral; Pl, pleural; and V, vertebral. The scale bars in the photographs equal 4 cm, and those in the drawings equal 2 cm.

Detailed descriptions, photographs, and schematic drawings of each of the anomalous specimens are presented here (Figures 1 and 2). The anomalies have been classified following the categorization proposed by Cherepanov [4] for the plates and scutes of the turtle shell (i.e., presence of additional plates and scutes, absence of regular plates and scutes, and unusual shapes of the plates and scutes). In most cases, the presence of an anomaly correlates with a compensatory growth of the adjacent elements (e.g., the presence of an additional plate or the absence of the regular one implicates a compensatory change in the shape or size of their adjacent plates; the same situation occurs in the case of anomalous scutes). In this sense, following Cherepanov [28], the anomalous plates or scutes that equate with compensatory growth are not treated as separate deviations as they are correlated with the anomalous adjacent plates or scutes. The morphogenetic cause of each type of abnormality is discussed, and current knowledge based on the study of anomalous extant turtles is considered, e.g., see [3,4,6,7,29–37].

3. Identification of Shell Deviations

3.1. Presence of Additional Plates and Scutes

The presence of additional shell elements corresponds to one of the most frequent abnormal variants identified here for *Pleurosternon bullockii* (Figures 1A–D and 2C–E), which is recognized for five different shell components (i.e., neural plates, costal plates, epiplastral plates, vertebral scutes, and gular-extragular scutes).

3.1.1. Additional Plates

The presence of additional plates on the neural series is recognized for three specimens (i.e., OUMNH K54009, Figure 1A; NHMUK OR 40960, Figure 1B; and NHMUK OR 43621, Figure 1C). As in other turtle taxa (e.g., [18,24]), these additional elements appear in *Pleurosternon bullockii* as minor abnormalities and have several configurations. Specifically, in the study sample, they correspond to an asymmetric ossification between two adjacent neurals (i.e., NHMUK OR 40960 and NHMUK OR 43621, Figure 1B,C) and to an additional neural medially divided into two asymmetrical ossifications (i.e., OUMNH K54009, Figure 1A). The additional plate is in the anterior region of the neural series of one individual, located near the posterior region of the first neural (i.e., NHMUK OR 43621, Figure 1C), whereas they are located in the posterior area of the series in the others (i.e., between the two posterior neurals in NHMUK OR 40960, Figure 1B, but at the contact between the neural series and the first suprapygal in OUMNH K54009, Figure 1A).

A deviation in the costal series is only identified for one specimen of *P. bullockii* (YPM VPPU 3364, Figure 1D), manifested as the development of one extraordinary pair of plates. This additional asymmetrical variant is located anteriorly to the first pair of costals, with the specimens showing nine pairs.

One additional plate has been observed in the plastron of a single specimen of *P. bullockii* (i.e., NHMUK R 1889, Figure 2E), located between both epiplastra. This small plate corresponds to a semicircular and medially symmetric element. It does not reach the entoplastron, but its anterior edge constitutes the most anterior plastral rim.

3.1.2. Additional Scutes

This category of shell anomalies is observed in the carapace of only one individual of *Pleurosternon bullockii*, corresponding to a juvenile (i.e., NHMUK 48263c, Figure 2C; see Guerrero and Pérez-García [38] for more details). The presence of additional vertebral scutes affects at least the first three of the elements of this series and is manifested by a longitudinal division that splits every scute in two, forming a double row of symmetrical elements.

Additional scutes have been observed in the plastron in two specimens of *P. bullockii* (i.e., NHMUK OR 44807, Figure 2D; NHMUK R 1889, Figure 2E). Additional plastral scutes are usually less common than carapace ones and are generally represented by small asymmetric elements [6,9–11,16,33], as in *P. bullockii*. Both anomalies are developed on the anterior plastral lobe of this species: medially, located between the gulars, extragulars, and humerals in NHMUK OR 44807 (Figure 2D), and laterally, between the left extragular and left humeral in NHMUK R 1889 (Figure 2E).

3.2. Absence of Regular Shell Plates

The absence of regular shell plates constitutes the less frequent shell deviation observed here among the individuals of *Pleurosternon bullockii*, manifested in only one of the specimens (i.e., NHMUK OR 28618, Figure 2B). In this individual, the fourth neural plate is completely absent. Consequently, the adjacent fourth pair of costal plates are expanded, contacting each other at the carapacial midline.

3.3. Unusual Shape of Plates and Scutes

The high morphological variability previously recognized for several plates and scutes of *Pleurosternon bullockii* (see [26,27]) makes it difficult to establish with certainty whether some plates and scutes shapes represent anomalies or extreme cases of individual variability. In this regard, three specimens of *P. bullockii* with abnormal scute shapes (i.e., OUMNH K54009, Figure 1A; NHMUK OR 47401, Figure 1F; and DORCM G6262, Figure 2F) and five specimens with anomalies in the shape of some plates (i.e., CAMSM J5327, 1E; NHMUK OR 47401, Figure 1F; CAMSM J5328, Figure 1G; NHMUK R 6880, Figure 1H; and NHMUK 24298, Figure 2A) are recognized as representing this category of shell anomalies.

3.3.1. Unusual Shape of Plates

Abnormal variations in the shape of the plates of *Pleurosternon bullockii* are observed in the neural series (i.e., CAMSM J5327, Figure 1E; NHMUK OR 47401, Figure 1F; CAMSM J5328, Figure 1G; NHMUK R 6880, Figure 1H; and NHMUK 24298, Figure 2A) and the first suprapygal (i.e., NHMUK OR 47401, Figure 1F). Most of these anomalies are developed in the posterior region of the carapace (Figure 1E–H), with the only exception being that recognized in NHMUK 24298 (Figure 2A). These anomalies are manifested as medially asymmetric (i.e., CAMSM J5327, Figure 1E; NHMUK OR 47401, Figure 1F; NHMUK R 6880, Figure 1H; and NHMUK 24298, Figure 2A) or almost symmetric plates (CAMSM J5328, Figure 1G). The anomalous region is in the posterior margin of several plates (i.e., CAMSM J5327, Figure 1E; the neural plate of NHMUK OR 47401, Figure 1F; and CAMSM J5328, Figure 1G), and both in the anterior and lateral ones of others (i.e., the suprapygal of NHMUK OR 47401, Figure 1F; NHMUK R 6880, Figure 1H; and NHMUK 24298, Figure 2A).

3.3.2. Unusual Shape of Scutes

Minor scute anomalies are identified in the morphology of the sulcus between the fourth and fifth vertebrals of three specimens of *Pleurosternon bullockii* (OUMNH K54009, Figure 1A; NHMUK OR 47401, Figure 1F; and DORCM G6262, Figure 2F). They are manifested as a markedly sinuous and asymmetric sulcus in two of them (OUMNH K54009, Figure 1A; NHMUK OR 47401, Figure 1F), whereas the sulcus is extremely anteriorly curved and medially symmetric in DORCM G6262 (Figure 2F). By contrast, in the non-anomalous specimens of *P. bullockii*, this sulcus is sub-straight (e.g., Figure 1G) or slightly curved and medially symmetric (e.g., Figure 1B,E). The sinuous sulcus of OUMNH K54009 and NHMUK OR 47401 overlaps two plates, belonging to the neural and the suprapygal series (Figure 1A,F), whereas the sulcus only overlaps the last element of the neural series in DORCM G6262 (Figure 2F). This latter condition coincides with that observed in the remaining *P. bullockii* specimens, in which the sulcus only overlaps one medial plate (i.e., the last neural or the first suprapygal; see [27]). Two of these anomalies are accompanied by deviations in the plates on which these scutes were located (see the explanation above and Figure 1A,F).

4. Discussion

4.1. Morphogenetic Origin of the Pleurosternon bullockii Shell Anomalies

A detailed analysis of articulated partial and complete shells of *Pleurosternon bullockii* evidenced that fourteen of more than sixty shells presented anomalies. None of them were the result of injury or disease.

4.1.1. Additional Plates

The presence of additional plates has been reported as an anomaly of morphogenetic origin for many species of extant turtles (e.g., neural [13,28,39] or costal plates [15,28,34,40]) and for some extinct ones (e.g., neural [18,21,24] or costal plates [17,19,41,42]). The appearance of small additional ossifications (i.e., intercalary plates sensu Cherepanov [4]), such as those observed here for the neural series (Figure 1A–C) and between both epiplastra

(Figure 2E) of some individuals of *Pleurosternon bullockii*, has been identified in the newborns of several extant turtle species [2,4,30,32]. Although they have been interpreted as originating in the regions where the fontanelles close more slowly, filling the region without ossification between the adjacent plates [28], this process (i.e., the closing of fontanelles and the formation of intercalary plates) cannot be confirmed for *P. bullockii*.

The presence of the additional first costal pair in YPM VPPU 3364 (Figure 1D) could be a consequence of an overgrowth of the anterior elements of the costal rib series and the existence of a contact between them and the dermal layer [3,4]. Likewise, this also could potentially be explained by the inclusion of an additional body segment (e.g., vertebra and ribs) into the shell, either homeotic shift resulting in a change in the identity of the eight presacral from cervical to dorsal [43] or just an extra segment in front of the normal first costal. However, since the visceral view of this specimen is not available, it is unknown which of these two hypotheses is the adequate.

Additional plates and scutes can also appear as a result of a shell damage (e.g., mechanical [44–47]). However, this hypothesis has been excluded for the anomalies of *P. bullockii* since the surface of the specimens shows no evidence of such damage.

4.1.2. Additional Scutes

As occurs for plates, the presence of additional scutes has also been commonly identified for several extant turtle clades ([7,9,10,12,33,48–50]) and some extinct ones [22]. One of the most common anomalies reported in the turtle shell is the presence of additional vertebrals, which can manifest in several asymmetrical and symmetrical patterns (e.g., [7,8,10–12,23,50]). These anomalous patterns have been observed in both extinct [22] and extant forms [12]. As demonstrated by morphogenetic and genetic data [2,7,33,36,37], vertebral scutes are formed as independent pairs of primordia that eventually fuse between them to generate single scutes [3,7,33]. The location of these scute primordia depends on the synchronized arrival of signaling molecules from both sides of the carapacial ridge [7]. Thus, the anomalous positioning of the carapacial ridge can generate an asymmetric pattern of the vertebral scutes or a failure of their fusion (e.g., [32,37]; see also Figure 8 in [7]). In this context, the symmetrical scute splitting recognized for the individual of *Pleurosternon bullockii* discussed here (Figure 2C) is identified as a consequence of a wide carapacial ridge [7], where there was too much distance between the scute primordia and, therefore, they lost the connection and started to form independent scutes [7,22,36]. The absence of connection between these elements could be partially influenced by the relative size of the vertebrals of some specimens since these have been described as relatively wide in relation to their length in several juveniles of *P. bullockii*. Thus, the specimens with wider vertebrals during the embryological development could be those that present more distance between the vertebral placodes and, therefore, a weaker lateral union between them.

The presence of small and irregular scutes (i.e., intercalary scutes sensu Cherepanov [3]) equivalent to those observed in the plastron of *P. bullockii* (Figure 2D,E) are commonly related to the existence of septal depressions free from scute anlagen, which are occupied with extraordinary placodes (i.e., focal regions of thickened epidermis), even in the case of minor disturbances during the embryonic development [3,6,33].

4.1.3. Absence of Regular Shell Plates

The reduction in the number of shell plates has been barely reported in extant and fossil turtles [4]. The exception are neural plates, in which the variation in the number has been commonly identified as an evolutionary trend for various turtle lineages or noted for some taxa of several lineages (e.g., [35]). However, it has also been observed as an anomaly for representatives of extant and extinct species (e.g., [13,15]), as occurs in the specimen of *Pleurosternon bullockii* NHMUK OR 28618 (Figure 2B). The variability in the number of neural plates, such as that observed in NHMUK OR 28618 in relation to the number of normal plates for its species, has been commonly associated with the number of connections between spinous processes of the vertebrae and the dermis of the carapace arising during the ontogenesis [4,28]. In the literature, common developmental mechanisms of neural plates in Testudines have been demonstrated [35]. Despite the embryogenesis process being unknown in the representatives of the turtle stem group, those mechanisms have been hypothesized as shared between all representatives of Testudinata [35]. Thus, this causal factor is attributed here as the more plausible hypothesis for the absence of the neural plate of NHMUK OR 28618.

4.1.4. Unusual Shape of Plates

Following the morphogenetic studies performed in extant turtles [4,28], anomalous morphological variations of the neural plates of *Pleurosternon bullockii* (Figures 1E–H and 2A) are interpreted here as the morphogenetic result of the unstable connection between the neural arches and the dermis in the posterior region of the carapace [4,28]. The anomalous morphology of the suprapygal of NHMUK OR 47401 (Figure 1F) is identified here as a result of a disturbance of the growth of that plate, as has been observed in some extant taxa [4]. This disturbance could be caused by the anomaly observed in the anterior margin of the fifth vertebral scute (see below) since the arrangement of the suprapygals, similar to that of the peripherals and the pygal, has been commonly associated with that of the previously formed carapace scutes [4,28].

4.1.5. Unusual Shape of Scutes

Embryological studies have demonstrated that the epidermal placodes corresponding to vertebral scutes develop relatively late during the morphogenesis, after those of the pleurals [2]. Consequently, anomalies in the shape of the vertebral scutes are commonly the result of the asymmetrical formation of the pleural scutes. Therefore, the final shape and size of the vertebrals are conditioned by the growth conditions (e.g., location [7], direction of growth [32], or number of contacts with other scutes [3,32]) of the pleural epidermal placodes. However, none of the three specimens of *Pleurostenron bullockii* analyzed here present asymmetrical pleurals Figures 1A,F and 2F. Therefore, the unusual shape of the vertebrals of *P. bullockii* is interpreted here as the main result of the asymmetrical formation of the vertebral placodes.

4.2. General Considerations of the Pleurosternon bullockii Shell Anomalies

The identification and the detailed study of the anomalies of *Pleurosternon bullockii* revealed that carapace abnormalities (i.e., 85% of the total anomalies detected here for the shell of *P. bullockii*) predominate over those of the plastron (i.e., 15% of the total anomalies), as described in many extant turtle representatives as a result of the basal mechanisms of morphogenesis [28], which produces higher stability in the plastron. Specifically, the plates of the neural series are the shell elements more susceptible to being affected by anomalies of morphogenetic origin. Likewise, the plate anomalies of *P. bullockii* do not have an impact on the arrangement and morphology of scutes (e.g., NHMUK OR 40960 and NHMUK OR 43621, Figure 1B,C) whereas, in accordance with other extant taxa [28], the anomalous arrangement of scutes can imply the disturbance of some carapacial plates [4], as could be the case for the suprapygal of NHMUK OR 47401 (Figure 1F). However, this last affirmation cannot be confirmed with certainty for *P. bullockii* due to this coincidence having only been observed in one specimen (Figure 1F). The independent development between plates and scutes has also been identified in most extant and extinct turtle taxa [7,9,51], except for testudinids, in which an association between such shell elements has been reported [51]. The anomalies observed in this study do not compromise the principal function of the carapace, which is the physical protection of the organism. Thus, in no case did these shell deviations cause severe selective disadvantages, since almost all of the anomalous specimens survived to the adult stage.

Over the years, several hypotheses have been developed to determine the etiology of morphogenetic anomalies of turtles. Thus, such deviations have been variously interpreted as atavistic recurrences that have been lost during phylogeny [9,52], embryonic mutations [10,11,53], or adverse environmental factors during embryonic development (e.g., extreme temperatures or humidity [1,5,7,14,18,36,54–57], and genetic diversity [12,18,49]). Currently, the combination of genetic and environmental factors as causative agents is the more accepted hypothesis [14,33,49]. Both factors (i.e., the environmental and the genetic one) are compatible with the possible etiologies that could have be caused the anomalies of *P. bullockii*. However, for the moment, the separation of genetic components from environmental effects in extant turtles has not been very successful [3,6]. Thus, it is not possible to infer the relative roles of genetic diversity and environmental factors in determining the anomalies for *P. bullockii* or any other extinct taxon.

5. Conclusions

The European turtle *Pleurosternon bullockii* is the best represented member of Pleurosternidae (Paracryptodira), being constituted by the largest numbers of shells for any turtle taxon in the Lower Cretaceous record of this continent. More than seventy articulated complete and partial shells of *P. bullockii* are identified, with most of them being from the Berriasian (Lower Cretaceous) of the Purbeck Group. Thus, the large availability of specimens as well as their good preservation has recently allowed for the characterization of the intraspecific variation in the species (i.e., individual variability, sexual dimorphism, and ontogeny). However, the extreme cases of morphological variation (i.e., anomalies) have not been analyzed, neither for *P. bullockii* nor for any other member of Paracryptodira.

In this context, the identification and the analysis of fourteen anomalous specimens of *P. bullockii* has allowed us to describe the distribution and frequency of the morphological deviations in the shell of this stem turtle, providing, for the first time, detailed data regarding the manifestation of this type of intraspecific variation both for Pleurosternidae as well as any other member of Paracryptodira. The results have revealed a predominance of carapace anomalies over those of the plastron. In particular, the plates of the neural series have been identified as shell elements more susceptible to the anomalies of morphogenetic origin. Likewise, the presence of additional shell elements as well as the unusual shape of some plates and scutes are the categories of anomalous variation that appear in more specimens of the study sample. In any case, none of the anomalies observed for *P. bullockii* should have compromised the principal function of the carapace of any of the specimens analyzed here, and therefore, they likely lacked negative consequences for their vital activity.

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Abbreviations

CAMSM	Sedgwick Museum, Department of Geology, University of Cambridge, UK
DORCM	Dorset County Museum, Dorchester, UK
NHMUK	Natural History Museum, London, UK
OUMNH	Oxford University Museum, Oxford, UK
YPM	Peabody Museum of Natural History, Yale University, USA

References

1. Mast, R.B.; Carr, J.L. Carapacial scute variation in Kemp's ridley sea turtle (*Lepidochelys kempi*) hatchlings and juveniles. In Proceedings of the First International Symposium on Kemp's Ridley Sea Turtle Biology, Conservation and Management, Galveston, TX, USA, 1–4 October 1989; pp. 202–219.
2. Cherepanov, G.O. Ontogenesis and evolution of horny parts of the turtle shell. *Russ. J. Herpetol.* **2006**, *1*, 19–33.
3. Cherepanov, G.O. Patterns of scute development in turtle shell: Symmetry and asymmetry. *Paleontol. J.* **2014**, *48*, 1275–1283. [CrossRef]
4. Cherepanov, G.O. Nature of the turtle shell: Morphogenetic causes of bone variability and its evolutionary implication. *Paleontol. J.* **2016**, *50*, 1641–1648. [CrossRef]
5. Loehr, V.J.T. Wide variation in carapacial scute patterns in a natural population of speckled tortoises, *Homopus signatus*. *Afr. J. Herpetol.* **2016**, *65*, 47–54. [CrossRef]
6. Moustakas-Verho, J.E.; Cherepanov, G.O. The integumental appendages of the turtle shell: An evo-devo perspective. *J. Exp. Zool.* **2015**, *324*, 221–229. [CrossRef] [PubMed]
7. Zimm, R. On the Development of the Turtle Scute Pattern and the Origins of Its Variation. Ph.D. Thesis, University of Helsinki, Helsinki, Finland, 20 February 2019.
8. Parker, G.H. Correlated abnormalities in the scutes and bony plates of the carapace of the sculptured tortoise. *Am. Nat.* **1901**, *35*, 17–24. [CrossRef]
9. Newman, H.H. The significance of scute and plate "abnormalities" in Chelonia. A contribution to the evolutionary history of the chelonian carapace and plastron, Part, I. *Biol. Bull.* **1906**, *10*, 99–114. [CrossRef]
10. Coker, R. Diversity in the scutes of Chelonia. *J. Morphol.* **1910**, *21*, 1–75. [CrossRef]
11. Lynn, W.G. Variation in scutes and plates in the box-turtle, *Terrapene carolina*. *Am. Nat.* **1937**, *71*, 421–426. [CrossRef]
12. Zangerl, R.; Johnson, R.G. The nature of shield abnormalities in the turtle shell. *Fieldiana Geol.* **1957**, *10*, 341–362.
13. McEwan, B. Bone anomalies in the shell of *Gopherus polyphemus*. *Fla. Sci.* **1982**, *45*, 189–195.
14. Velo-Antón, G.; Becker, C.G.; Cordero-Rivera, A. Turtle carapace anomalies: The roles of genetic diversity and environment. *PLoS ONE* **2011**, *6*, e18714. [CrossRef] [PubMed]
15. Farke, C.M.; Distler, C. Ontogeny and abnormalities of the tortoise carapace: A computer tomography and dissection study. *Salamandra* **2015**, *51*, 231–244.
16. Saçdanaku, E.; Haxhiu, I. Accessory scutes and asymmetries in European pond turtle, *Emys orbicularis* (Linnaeus, 1758) and Balkan terrapin, *Mauremys rivulata* (Valenciennes, 1833) from Vlora Bay, western Albania. *Int. J. Fauna Biol. Stud.* **2016**, *3*, 127–132.
17. Hay, O.P. *The Fossil Turtles of North America*; Carnegie Institution of Washington Publication No. 75: Washington, DC, USA, 1908; p. 568.
18. Zangerl, R.; Turnbull, W.D. *Procolpochelys grandaeva* (Leidy), an early carettine sea turtle. *Fieldiana Geol.* **1955**, *37*, 345–382.
19. Weems, R.E. Middle miocene sea turtles (*Syllomus*, *Procolpochelys, Psephophorus*) from the Calvert formation. *J. Paleontol.* **1974**, *48*, 278–303.
20. Brinkman, D.B.; Nicholls, E.L. Anatomy and relationships of the turtle *Boremys pulchra* (Testudines: Baenidae). *J. Vertebr. Paleontol.* **1991**, *11*, 302–315. [CrossRef]
21. Sullivan, P.M.; Joyce, W.G. The shell and pelvic anatomy of the Late Jurassic turtle *Platychelys oberndorferi* based on material from Solothurn, Switzerland. *Swiss J. Palaeontol.* **2017**, *136*, 323–343. [CrossRef]
22. Szczygielski, T.; Słowiak, J.; Dróżdż, D. Shell variability in the stem turtles *Proterochersis* spp. *PeerJ* **2018**, *6*, e6134. [CrossRef] [PubMed]
23. Garbin, R.C.; Böhme, M.; Joyce, W.G. A new testudinoid turtle from the middle to late Eocene of Vietnam. *PeerJ* **2019**, *7*, e6280. [CrossRef]
24. Joyce, W.G.; Rollot, Y.; Cifelli, R.L. A new species of baenid turtle from the Early Cretaceous Lakota Formation of South Dakota. *Foss. Rec.* **2020**, *23*, 1–13. [CrossRef]
25. Owen, R. Report on British fossil reptiles. Part II. *Rep. Br. Ass. Advmt. Sci.* **1842**, *11*, 60–204.
26. Guerrero, A.; Pérez-García, A. On the validity of the British Upper Jurassic turtle "*Pleurosternon portlandicum*" (Paracryptodira, Pleurosternidae). *J. Iber. Geol.* **2020**, *46*, 419–429. [CrossRef]
27. Guerrero, A.; Pérez-García, A. Morphological variability and shell characterization of the European uppermost Jurassic to lowermost Cretaceous stem turtle *Pleurosternon bullockii* (Paracryptodira, Pleurosternidae). *Cretac. Res.* **2021**, *125*, 104872. [CrossRef]
28. Cherepanov, G.O. Anomalies of the bony shell of turtles. *Zool. Zhurnal* **1994**, *73*, 68–78.

29. Cherepanov, G.O. New morphogenetic data on the turtle shell: Discussion on the origin of the horny and bony parts. *Stud. Palaeocheloniol.* **1989**, *3*, 9–24.
30. Cherepanov, G.O. Ontogenetic development of the shell in *Trionyx sinensis* (Trionychidae, Testudinata) and some questions on the nomenclature of bony plates. *Russ. J. Herpetol.* **1995**, *2*, 129–133.
31. Cherepanov, G.O. The origin of the bony shell of turtles as a unique evolutionary model in reptiles. *Russ. J. Herpetol.* **1997**, *4*, 155–162. [CrossRef]
32. Cherepanov, G.O. Scute's polymorphism as a source of evolutionary development of the turtle shell. *Paleontol. J.* **2015**, *49*, 1635–1644. [CrossRef]
33. Cherepanov, G.; Malashichev, Y.; Danilov, I. Supernumerary scutes verify a segment-dependent model of the horny shell development in turtles. *J. Anat.* **2019**, *235*, 836–846. [CrossRef]
34. Kordikova, E.G. Paedomorphosis in the shell of fossil and living turtles. *Neues Jahrb. Geol. Palaontol. Abh.* **2000**, *218*, 399–446. [CrossRef]
35. Scheyer, T.M.; Brüllmann, B.; Sánchez-Villagra, M.R. The ontogeny of the shell in side-necked turtles, with emphasis on the homologies of costal and neural bones. *J. Morphol.* **2008**, *269*, 1008–1021. [CrossRef] [PubMed]
36. Moustakas-Verho, J.E.; Zimm, R.; Cebra-Thomas, J.; Lempiainen, N.K.; Kallonen, A.; Mitchell, K.L.; Hamalainen, K.; Salazar-Ciudad, I.; Jernvall, J.; Gilbert, S.F. The origin and loss of periodic patterning in the turtle shell. *Development* **2014**, *141*, 3033–3039. [CrossRef] [PubMed]
37. Moustakas-Verho, J.E.; Cebra-Thomas, J.; Gilbert, S.F. Patterning of the turtle shell. *Curr. Opin. Genet. Dev.* **2017**, *45*, 124–131. [CrossRef] [PubMed]
38. Guerrero, A.; Pérez-García. Ontogenetic development of the European basal aquatic turtle *Pleurosternon bullockii* (Paracryptodira, Pleurosternidae). *Foss. Rec.* **2021**. accepted.
39. Webb, R.G. *North American Recent Soft-Shelled Turtles (Family Trionychidae)*; University of Kansas Publications, Museum of Natural History: Lawrence, KS, USA, 1962; Volume 13, pp. 429–611.
40. Pritchard, P.C.H. Evolution and structure of the turtle shell. In *Biology of Turtles*; Wyneken, J., Godfrey, M.H., Bels, V., Eds.; CRC Press: Boca Raton, FL, USA; London, UK; New York, NY, USA, 2008; pp. 46–83.
41. Gaffney, E.S.; Hutchison, J.H.; Jenkins, F.A.; Meeker, L.J. Modern turtle origins: The oldest known cryptodire. *Science* **1987**, *237*, 289–291. [CrossRef]
42. Brinkman, D.B. Anatomy and systematics of *Plesiobaena antiqua* (Testudines; Baenidae) from the mid-Campanian Judith River Group of Alberta, Canada. *J. Vertebr. Paleontol.* **2003**, *23*, 146–155. [CrossRef]
43. Szczygielski, T. Homeotic shift at the dawn of the turtle evolution. *R. Soc. Open Sci.* **2017**, *4*, 160933. [CrossRef] [PubMed]
44. Gadow, H. On the reproduction of the *carapax* in tortoises. *J. Anat.* **1886**, *20*, 220–224.
45. Smith, H.M. Total regeneration of the carapace in a box turtle. *Turtox News* **1958**, *36*, 234–237.
46. Rose, F.L. Carapace regeneration in Terrapene (Chelonia: Testudinidae). *Southwest Nat.* **1986**, *31*, 131–134. [CrossRef]
47. Kuchling, G. Restoration of epidermal scute patterns during regeneration of the chelonian carapace. *Chelonian Conserv. Biol.* **1997**, *2*, 500–506.
48. Ayres Fernández, C.; Cordero Rivera, A. Asymmetries and accessory *scutes* in *Emys orbicularis* from Northwest Spain. *Biologia* **2004**, *59*, 85–88.
49. Cordero Rivera, A.; Ayres, C.; Velo-Antón, G. High prevalence of accessory *scutes* and anomalies in Iberian populations of *Emys Orbicularis*. *Rev. Esp. Herp.* **2008**, *22*, 5–14.
50. Mlynarski, M. *Studies on the Morphology of the Shell of Recent and Fossil Tortoises*; Państwowe Wydawnictwo Naukowe: Warsaw, Poland, 1956; Volume 1, pp. 1–16.
51. Cherepanov, G.O. Morphogenetic and constructional differences of the carapace of aquatic and terrestrial turtles and their evolutionary significance. *J. Morphol.* **2019**, *280*, 1571–1581. [CrossRef] [PubMed]
52. Gadow, H. Orthogenetic variation in the shells of Chelonia. In *Zoological Results Based on Material from New Britain, New Guinea, Loyalty Islands and Elsewhere, Collected during the Years 1895, 1896, and 1897*; Willey, A., Ed.; University Press: Cambridge, UK, 1899; Part 3; pp. 207–222.
53. Frye, F.L. *Biomedical and Surgical Aspects of Captive Reptile Husbandry*; Krieger Publications: Malabar, FL, USA, 1991; p. 637.
54. Lynn, W.G.; Ullrich, M.G. Experimental production of shell abnormalities in turtles. *Copeia* **1950**, *1950*, 253–262. [CrossRef]
55. Özdemir, B.; Türkozan, O. Carapacial scute variation in green turtle, *Chelonia mydas* hatchlings in Northern Cyprus. *Turk. Zool. Derg.* **2006**, *30*, 141–146.
56. Bujes, C.S.; Verrastro, L. Supernumerary epidermal shields and carapace variation in Orbigny's slider turtles, *Trachemys dorbigni* (Testudines, Emydidae). *Rev. Bras. Zool.* **2007**, *24*, 666–672. [CrossRef]
57. Caracappa, S.; Pisciotta, A.; Persichetti, M.F.; Caracappa, G.; Alduina, R.; Arculeo, M. Nonmodal scutes patterns in the Loggerhead Sea Turtle (*Caretta caretta*): A possible epigenetic effect? *Can. J. Zool.* **2016**, *94*, 379–383. [CrossRef]