The "Midventral Keel" in Testudinata

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The origin of the Testudinata is much in doubt, but several scientists have reconstructed an ancestor from the evidence afforded by paleontology, embryology, comparative anatomy, and "atavistic" scutes.

Probably less has been written about the hypothetical undershell or plastron than about most parts of the turtle. However, in place of the midventral seam or suture common to reptiles, it was the belief of several scientists that there had been a single midventral row of bone plates covered by horn scutes on the plastron. In other words, if one could see the under shell of the ancestral turtle he would behold not a central seam or suture, but a central row of horny scutes or scales, possibly in the form of a tuberculated ridge or keel flanked by similar parallel keels, somewhat as is shown in Figure 1.

Newman advanced three theories to prove this. The first was that the midventral keel now found in the many-keeled leather-backed marine turtle is a remnant of an ancestral keel no longer found in other turtles; the second, that certain mid-areas under the tail-trunk of the snapping turtle were homologous to this midventral row; and the third, that single intergulars and the uncommon interplastrals of modern turtles were atavistic reminders of an ancient structure. Hay also believed in a midventral row, but advanced only the third point above mentioned.[1]

In order to show that it is probable that the ancestral turtle possessed a median seam or suture, as is the case in modern reptiles, and not a midventral row of bones and scutes, we must be able to account for the presence of a single midventral row of scutes in snakes, the midventral keel in the great marine turtle, and the occasional intergular and interplastrals of pond turtles, and then present such further evidence as we possess.

Snakes are the only reptiles which have a midventral row of scutes. These crawling reptiles are a comparatively modern development and can hardly be claimed to have had a common ancestor with the ancient turtle. There is sufficient evidence that the single ventrals and caudals of snakes are a fusion of several rows (Grant, 1935). Many species have a double row of scutes under the tail with a consequent median suture. The tail, having least to do with the gliding locomotion of snakes, would be expected to be the last place to retain a median suture, and that is exactly the case. One or more pairs of preanals in various species again remind one of a primitive central suture. Young snakes usually have several scutes divided at the midline at the umbilical

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[1]Direct quotations from these writers follow: Newman (1906, W. 75): "The missing keel (of modern turtles) is the midventral one (of the leather-backed turtle)"; (p. 102): "Smaller and less regular rows of tubercles and scales (on the tail-trunk of the snapping turtle) are homologized with the secondary or lost rows (of turtle scutes) as follows . . . interplastrals (of the tail-trunk of the snapping turtle being homologous to the vanished interplastrals of the ancestral turtle.)"; and (p. 71; see also pp. 75, 81, 103, and 111): "Traces of a median ventral row of scutes are found normally in some species—I have given the name *"interplastral"* to this row. A single (anterior) median scute is named the *"intergular."* O. P. Hay (1898); "The great scutes of the plastron . . . grow toward the midline . . . they have suppressed the scutes of the middle keel."; and (Hay, 1928): "The median, or interplastral row of epithecal bones with their scutes, were early suppressed."

region.   Occasional atavistic ventral scutes start from one side and
stop at the midline.   Other specimens have a notch or nick at the center
of many of the ventrals.   Newman (1906, p. 107, and note 6) has shown
that color pattern is closely associated with the centers of existing or lost
scutes in turtles.   The same law probably holds true with snakes, as
none have a median line of pigmented dots or marks, but many have
parallel rows of dots or other markings, leaving the midline clear.   This
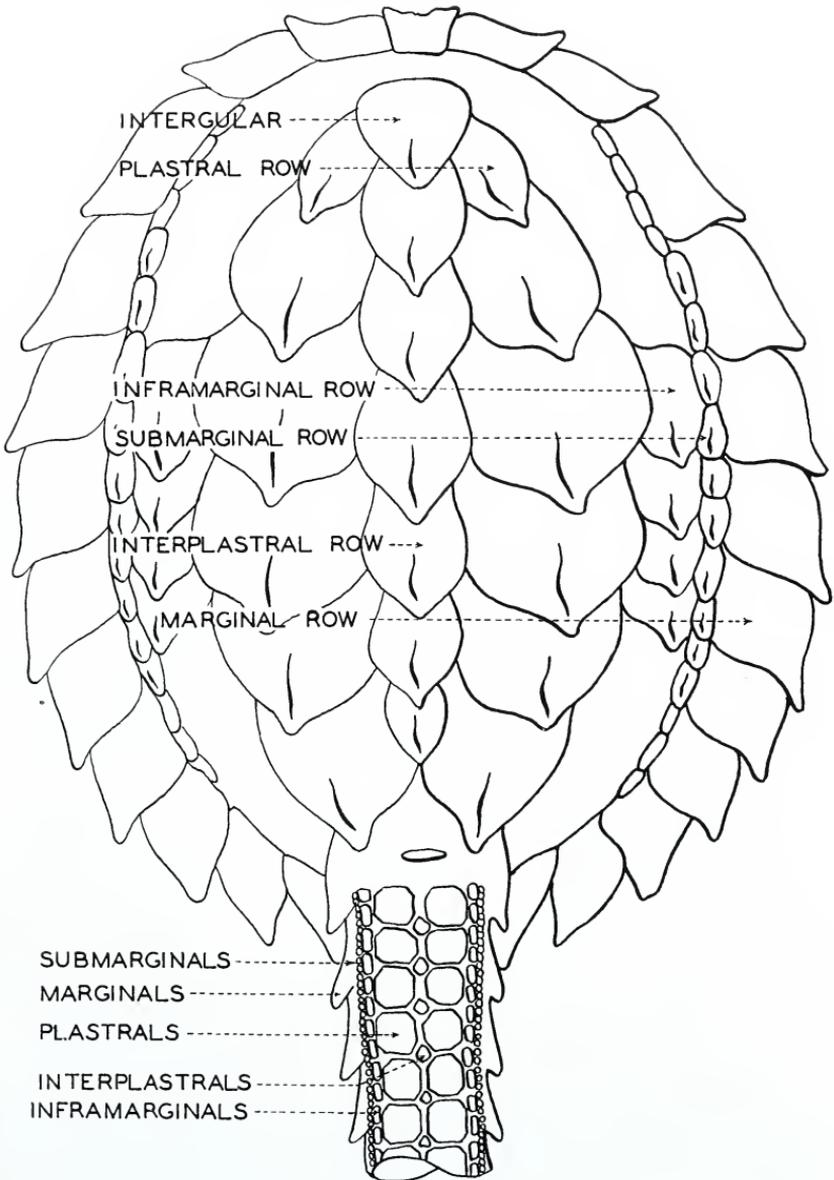

Fig. 1. A composite hypothetical plastron from various writers.

would indicate an ancestral suture flanked by several rows of scutes all of which have fused into the present wide ventrals of snakes. The snake, then, is the only modern reptile with a median row of scutes, and this development was probably coeval with limbless locomotion. All other reptiles have a median suture.

The midventral keel in Dermochelys, the leather-backed turtle, must be explained. It is difficult to imagine any reason for a terrestrial animal's having prominent ventral keels, especially an animal with the low clearance of a turtle. It seems reasonable therefore to believe that the leather-backed turtle developed its five ventral keels after becoming aquatic. Why a marine turtle should develop so many keels is possibly because all terrestrial quadrupeds normally progress by moving the front feet forward alternately with the diagonal hind foot. Pond turtles swim as they walk—diagonal legs moving in unison to hold their direction; but marine turtles swim with the fore flippers in unison, the hind flippers not being used in straight progression. Therefore, there must have been a time when the marine turtle was changing methods from swimming with alternate legs to its present system. If at any time it swam with alternate front appendages without a corresponding impetus from the diagonal hind ones its motion would have been oscillating. Keels would help overcome such an oscillation. The foregoing rather fantastic theory is given as much to call attention to the interesting problem of the different motions of the limbs of pond and marine turtles as to explain the presence of keels. A better reason for ventral keels might be for protection from attack from underneath. The hawksbill turtle has ventral keels, but not a median row or keel. The other marine turtles apparently learned to swim without keels or at least have not retained any trace of them. In the final analysis, as Baur (1888, p. 144) said, "Sea turtles have been developed in different places at different times . . ."; so an explanation for one genus might not hold for another.

To explain the origin of the central areas under the tail-trunk of *Chelydra*, the snapping turtle, it is noted that large scutes in reptiles seldom fit together in square points. Thus the square scutes of crocodilians have the tips rounded off and the resulting interstices filled by "pseudo-scutes" or merely criss-crossed skin. It has been shown (Grant,
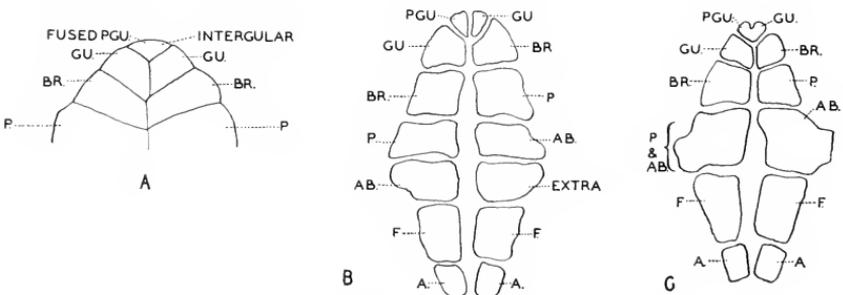

Fig. 2. Comparative interpretation of scutes. *PGU*, pregular; *GU*, gular; *BR*, brachial; *P*, pectoral; *AB*, abdominal; *F*, femoral; *A*, anal. The letters on the left of each figure are the writer's interpretation; those on the right are the interpretations of Coker in A, and Newman in B and C, from whom the figures are taken. The difference is due to the writer's naming the scutes from the center, whereas others name them from the anterior end, starting always with a gular.

1937) that the plastral scutes in very old turtles sometimes have their corners cut off as a result of meandering sutures, which gives the appearance of interplastrals. The so-called median row of scutes on the underside of the tail of the snapping turtle, which Newman (1906, p. 102) homologizes with the lost theoretical midrow of bones and scutes of ancient turtles, is apparently no more than "fillers" between approximately square scutes, developed because lateral flexibility is necessary and would be impeded if the scutes impinged with right angles to their very points.

The "intergular" (Figure 2, A) is a single scute which has been designated as evidence of a lost median row. Newman (1906, p. 71) thus defines it: "A single (anterior) median scute is named the 'intergular'." That is satisfactory for a definition, but later he says (p. 93): "Fig. . . . shows . . . the gulars have been fused into a single median element." This is correct, but his Figures 52 and 53, which are our Figures 2, *B* and *C*, show the "intergular" divided and partly divided respectively. In other words, the intergular has been derived from a pair of scutes. It seems strange that, having fused, the resulting element called the "intergular" should then be held to represent a relic of a single median structure. The writer submits the divided intergular as evidence of an original double row and not as a representative of a lost single row. Coker (1910, p. 3) says: "In 31 new-born green turtles . . . the normally unpaired intergular was in 6 specimens represented by a pair of scutes and in 9 others was partially divided." Sixteen out of thirty-one seems to be a small percentage to prove normalcy. In other words, when a single median anterior unit is found, it is called an "intergular" and is used as evidence of a prior single median row. It would seem well to say that the anterior elements or "progulars" actually represent a pair of scutes of the interplastral rows.

Interplastrals are referred to as atavisms of a single midventral row when they occur singly, but when they occur in pairs, nothing is said about it. Newman (1906, p. 81) says: "The primitive condition
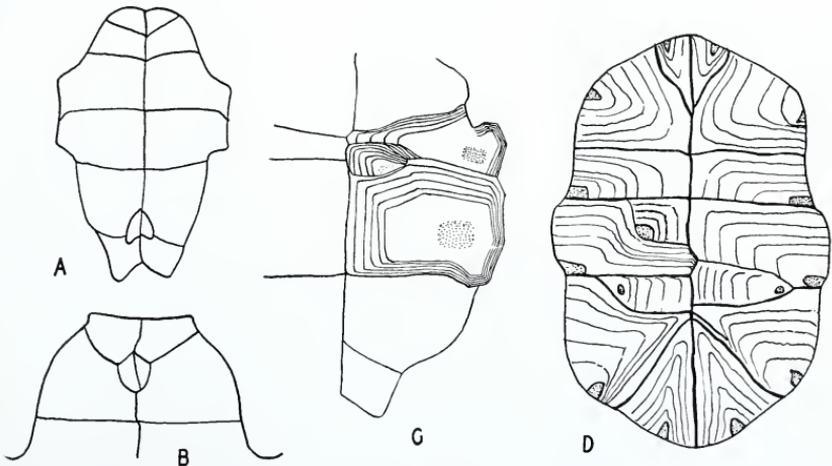

Fig. 3.   Evidence of a double interplastral row.   *A*, interfemorals;   *B*, interbrachials;   *C*, interpectoral;   *D*, interabdominal and interfemorals.

was probably one in which a scute was present at each point of union of four plastral scutes." It is difficult to see how his "intergular" could qualify by fitting between four plastrals since it touches only the gulars. He illustrates with figures of specimens bearing extra scutes in four of the five possible symphyses, and, strange to say, one of his figures shows a *pair* of interplastrals, the rest showing only single ones (Fig. 3, A). We strengthen this evidence by two more examples with paired interplastrals (Fig. 3, *B* and *D*) and one single, but lateral, interplastral (Fig. 3, *C*).

The pectoral and abdominal scutes normally join or bridge the plastron to the carapace in pond turtles, as shown in Figure 3, A. The writer believes that this is the most logical place to start classifying the plastral scutes and that they should be identified from this point forward and backward. The diagrams in Figure 2 are lettered according to our interpretation on the left side and according to the writers from whom the diagrams are borrowed, on the right hand side. In Figure 2, *B*, we have labelled the bridge scutes pectoral and abdominal respectively, and in Figure 2, *C*, we consider that the large bridging scute is formed by fusion of the pectorals and abdominals. Counting forward from this point in Figure 2, *B*, we find the brachials and then the gulars. Anterior to the gulars is another pair of scutes which we consider to represent an earlier normal anterior pair of plastral scutes. Lacking a name we call them *progulars*. Newman interprets them differently. He begins anteriorly and, in Figure 2, *B*, names the anterior pair gulars, then follow brachials, pectorals, and abdominals, and then ". . . a well-developed pair of extra scutes between the abdominals and femorals . . .", femorals, and anals. In Figure 2, *C*, we consider that the most anterior

element is formed from partly fused progulars, then gulars, brachials, fused pectorals and abdominals, femorals, and anals. Newman interprets them as beginning with partly fused gulars followed by brachials, pectorals, abdominals, femorals, and anals.

Further evidence against a midventral row of scutes or a keel may be had by studying the structure of keels that occur elsewhere on turtles. Keels on the upper shell or carapace of turtles occur only over the center of a row of bony plates, and they are frequently underlaid by a row of bone ossicles which may have been the bone cores of the tuberculated keels. A midventral scute-keel on the plastron of a turtle would presuppose the existence of a central row of underlying bones, but none such is shown ever to have existed. Again, one might expect that a row of ossicles would designate the position where the tubercles had been, as they do on the carapace of several species, but, again, no such evidence exists. Furthermore, a midventral keel
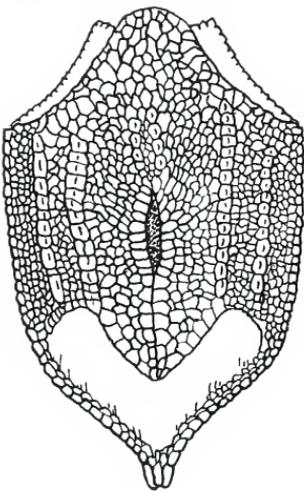
Fig. 4. Evidence that the midventral keel in the leather-backed turtle is postnatal. Newly-hatched young showing open umbilical scar and evidence that the keel is formed from the edges of this scar (after Stegneger, 1904).

means the formation of a scute-keel over a bone suture, and there is no such structure elsewhere on the turtle. The very nature of the development of a reptilian embryo is of a ventral suture which fuses, leaving a permanent seam, except in snakes, unbridged by bone or scute in the region of the umbilicus.

Finally, the midventral "keel" in the trunk-backed turtle is *postnatal* in development, as is shown in Figure 4, where the central keel is seen to be derived from the union of the thickened edges of the umbilical scar, which extends three quarters of the length of the plastron.
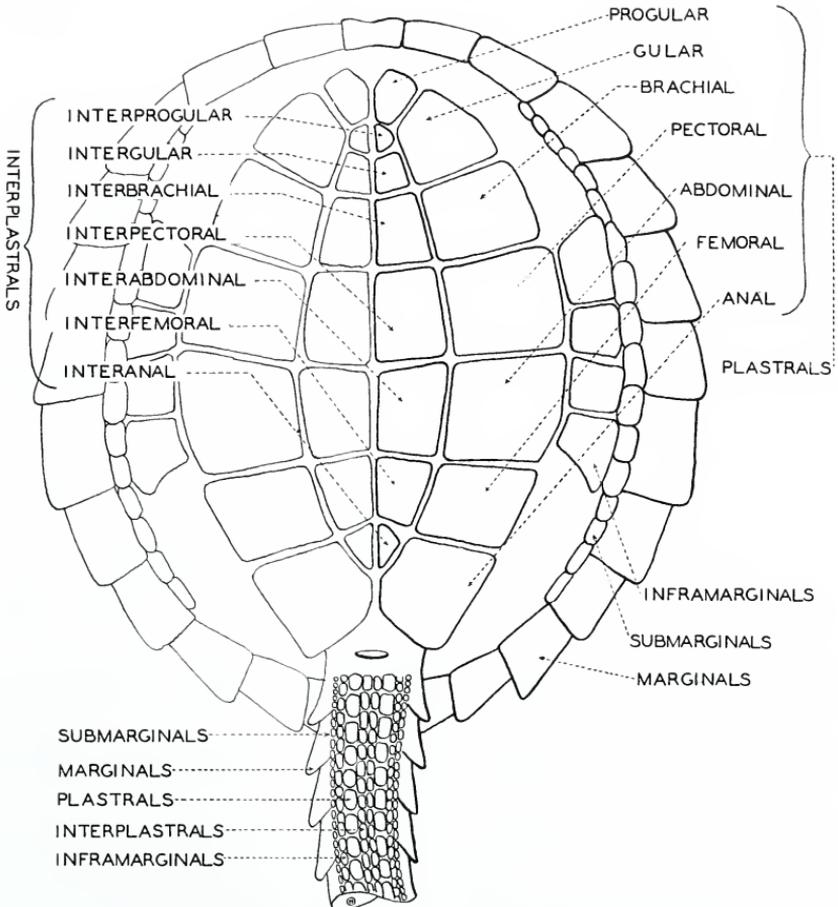

Fig. 5. Hypothetical plastron as reconstructed by the writer.

The writer believes that Figures 3, *A*, *B*, *C*, and *D*, show that there has been a crowding out, as Hay said, but that what was crowded out was a double row and not a single midventral row. He believes that an ancestral plastron and tail-trunk might have looked something like Figure 5 and recommends the adoption of the new nomenclature given in his figures wherever they add clarity. Comparing Figure 5 with Figures 2,

B and 3, it will be noted that actual examples are given for all scutes of the theoretical double interplastral row except the last interanal. It is expected that wider collecting may bring the missing case to light.

All the drawings used in illustrating this paper were made by Mr. Norman Bilderbach, by courtesy of Dr. C. G. Abbott, San Diego Society of Natural History.

Summary

1.   The theory has been advanced that ancient Chelonians possessed a single midventral row of plates and scutes, based on the following evidence: the midventral keel in Dermochelys, the mid-areas under the tail-trunk of Chelydra, and the single intergular and uncommon interplastrals.

2.   It is shown that, although the snake possesses a midventral row of scutes, this is a recent modification, that the midventral keel of *Dermochelys* is a post-natal modification of the umbilical scar, that the areas under the tail-trunk of *Chelydra* are pseudo-scutes or fillers, that the intergular is a result of the fusion of a pair of scutes, and that interplastrals are remnants of paired scutes.

3.   It is shown that it is improbable, for structural reasons, that there ever was a midventral row or keel.

4.   Figures are given illustrating the two hypothetical cases—the single-rowed plastron and tail-trunk and the double-rowed—also cuts showing the progulars and interplastrals and the umbilical region of a young Dermochelys showing the formation of the midventral keel.

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