ISSN: 0211-8327 Studia Geologica Salmanticensia, 41: pp. 29-37

ABOUT THE STRUCTURE OF THE AXIAL ELEMENTS OF TURTLE SHELL

[Sobre la estructura de los elementos axiales del caparazón de los quelonios]

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(FECHA DE RECEPCIÓN: 2004-12-09) (FECHA DE ADMISIÓN: 2005-01-07)
BIBLID [0211-8327 (2004) 41; 29-37]

RESUMEN: Un estudio comparativo del área axial en el espaldar de quelonios demuestra que la posición de los tipos específicos de placas neurales sigue ciertas reglas. Se muestra que los diversos patrones de placas neurales dependen de la forma del caparazón. Por lo tanto la colocación de los variados tipos que forman el área axial de los quelonios tiene solamente un valor taxonómico restringido.

Palabras clave: Quelonios, morfología comparada del espaldar, nucal, neurales, metaneurales, pigal.

ABSTRACT: A comparative study of the axial area in turtle shells shows that the position of the specific types of neurals follows certain rules. It can be shown, that the divers patterns of neurals depend on the form of the carapace. Consequently the arrangement of these divers types which form the axial area has only a restricted taxonomic value.

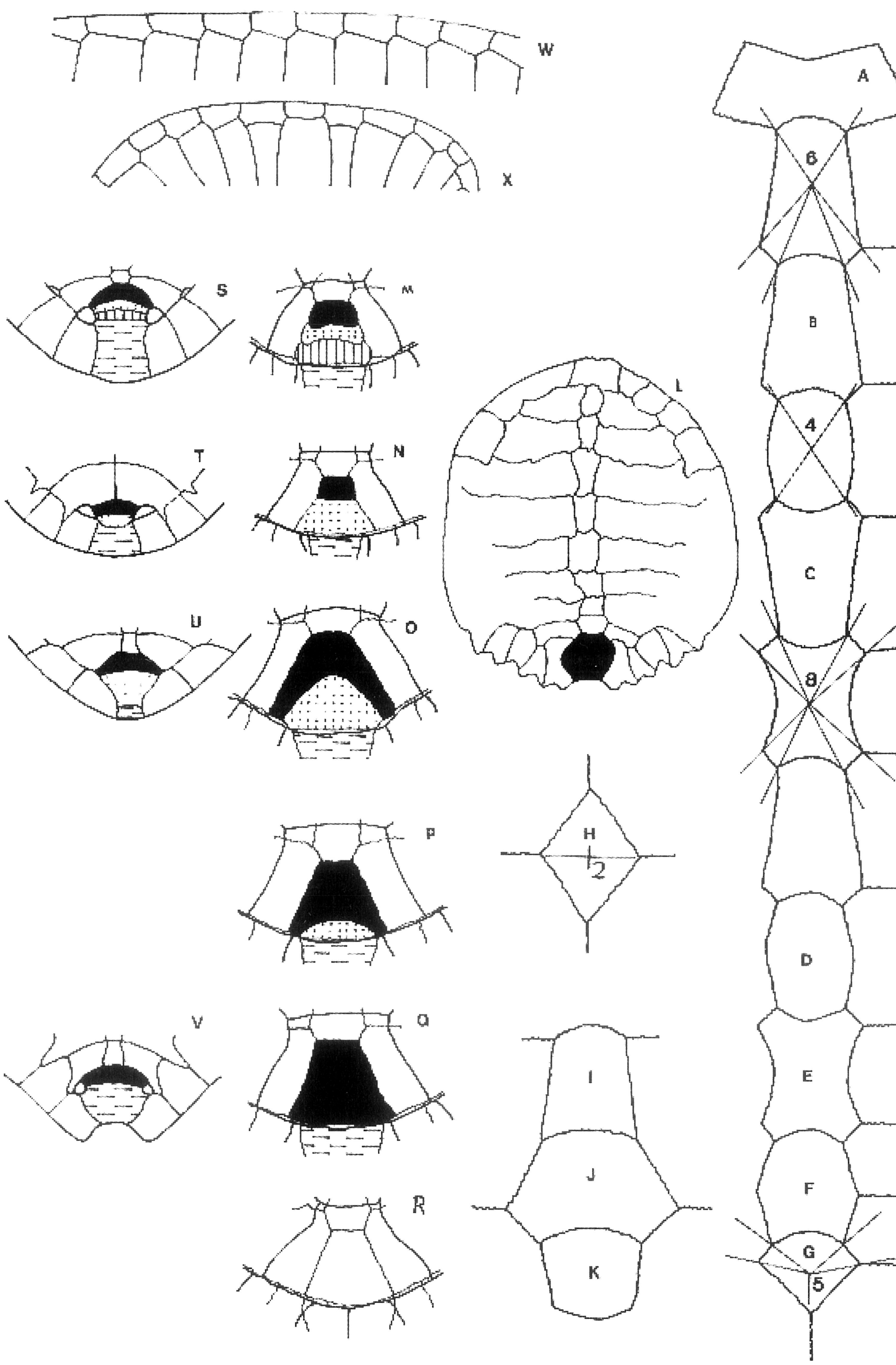
Key words: Turtles, comparative shell morphology, nuchalia, neuralia, metaneuralia, pygal-plate.

1. INTRODUCTION

The carapace of modern turtles consists of the following skeletal elements such as thoracal vertebrae, trunc vertebrae, lumbar vertebrae, and sacral vertebrae, as well as ribs which are fused with the ossified dermal plates. During evolution this carapace will be gradually reduced in divers groups. In some this primary thecal carapace is almost completely lost and a secondary epithecal-carapace is developed.

The ontogenetic trend towards reduction is shown by the decrease of plates. The ossified carapace of turtles is composed by a nuchal plate (Nu), neurals (NI-VIII), metaneurals (MNI-II or III), and a pygal plate (P). Lateraly situated, at both sides there are the pleurals (Pl I-VIII) and, at their circumference are the peripherals (Pe I-XI). Above the ossified carapace there are horny shields which are put together of a sequence of a cervical shield (C), central shields (Ce 1-5), caudals (Ca), lateral shields (L 1-4), and marginal shields (M 1-11). The ossified plastron consists of an entoplastron (ento), epilastral plates (epi), hyoplastrals (hyo), hypoplastrals (hypo), and xiphiplastrals (xiphi). At the ventral side of the plastron are pairs of horny gular shields (G). In some rare cases there is also a single intergular shield (IG), humerals (H), pectorals (P), abdominals (Ab), femorals (F), and anal shields (An). The connection between carapace and plastron usually is formed by bridges. The shape and the number of neurals or metaneurals has been considered important for systematic studies, but these elements are very variable (Pritchard, 1988; Staesche, 1961). General and synoptic remarks on the carapace are given by Broadley (1983), Mlynarski (1976), Pritchard (1979), Romer (1956) and Zangerl (1969).

Figure 1. A-nuchal plate, B-hexagonal plate 6P, C-hexagonal plate 6A, D-tetragonal plate, E-octagonal plate, F-hexagonal plate 6B, G-pentagonal plate, H-bigonal plate, I -metaneural plate I, J-metaneural plate II, K-pygal plate, L-carapace of Baena nodosa *with fused metaneurals and pygal (black), M-pygal region of* Testudo graeca *with an atavism in origin three metaneurals, N-M-pygal region of* Testudo graeca *with two metaneurals like in emydids (commonly "testudinoid"), O-M-pygal region of* Testudo graeca *with boomerang-like MN I (commonly "geochelonoid"), P-M-pygal region of* Testudo graeca *with very reduced MN II, Q-M-pygal region of* Testudo graeca *with fused metaneurals, R-M-pygal region of* Testudo hermanni *like that of* Testudo graeca *in Q, S-M-pygal region of* Thalassemys hugii *like the type of figure M, T-M-pygal region of* Idiochelys fitzingeri *like the type of figure N, U-M-pygal region of* Plesiochelys etalloni *like the type of figure O, V-M-pygal region of* Eurysternum wagleri *like the type of figure Q, W-correlation of hexagonal row with a flat carapace, X-correlation of the tetragonal/octagonal row with a domed shell. According Staesche (1961): M-R, Joyce (2000): S-V, Wiman (1933): L, and original A-H and W-X.*


W
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2. CHARACTER ANALYSIS

2.1. THE NUCHAL PLATE

The first plate of the axial row of the carapace is present in all hitherto known turtles since the Triassic genus *Proganochelys* up to the recent species (figure 1, A). It is a polygonal shaped plate with an anterior nuchal incision and a concave incision towards the first neural plate. The nuchal plate even occurs in species with an advanced reduction of the carapace, as it is true in dermochelyids and trionychins. In the last one the nuchal plate is pteriform with a small lateral processus. Some species have an isolated nuchal plate, and in *Dermochelys* it is the only concerned ossified element of the thecal-carapace.

2.2. TYPES OF NEURALS AND THE STRUCTURE OF THEIR ROW

The original number of neurals is ten which is conserved in the oldest turtles. Whereas in modern representatives usually eight are developed, but this is a very variable feature. According to the symmetrical organisation of the Chordata, the construction plan of the carapace and the medianelements are also symmetric. That means that generally speaking all neurals have the tendency for polygons with even edges. Assymetric neurals only exist in areas of reduction within the neural row. Six types of neurals can be distinguished which seem to be constant during ontogenesis.

2.2.1. Hexagonals

The main criterion is the orientation of the short lateral side of the neural, in orientation along the body axis. This original form includes two pairs of different long lateral sides:

1. 6P = short side posterior (P = posterior) (figure 1, 6, B) or:
2. 6A - short side anterior (A = anterior) (figure 1, C).

The margin beteen the long sides is convex, in contrary to those of the short one which is concave. Hexagonals which show the same length at the anterior and posterior side, are called 6B (B = both) (figure 1, F). There transversal side is more or less even.

Character code in this analysis: 6P = A, 6A = C, 6B = E.

2.2.2. Tetragonals

This derived type shows four convex sides (figure 1, 4, D). Rectangular plates are the most primitive, and the quadratic ones originate from the former. Tetragonals may derive from the hexangular 6P through the loss of two edges.

Character code in this analysis: 4 = B.

2.2.3. Octagonals

Again, this type of plate is of a secondary origin and shows four long sides at which the primary four edges have been elongated and doubled (figure 1, 8, E). Between these pairs at the edges short diagonal sides are developed. Tetragonals and octagonals are evolved from two neighbouring hexagonals either by loss or by summation of two edges.

Character code in this analysis: 8 = D.

2.2.4. Trigonals and pentagonals

Both types only occur as endplates of reduced neural rows, e.g. in *Pelusios* (figure 1, 5).

2.2.5. Bigonals

As a result of the reduction process, bigonals exclusively occur as separate single plates which are typically known in Cyclanorbines (figure 1, 2, H).

2.2.6. Combination of the neurals

In relation to the given basic shape of individual types of neurals only certain types of combinations are possible (figure 1, A-K). The divers combination of different shapes of single neural plates causes specific outlines of the distal part of the neural row. According to the shape of this distal line, corresponding outlines of the distal side of pleurals are required. Wedge formed pleurals insert at the distal side of tetragonals and octagonals (figure 1, X). Whereas pleurals which connect with hexagonals, have a broaden proximal side (figure 1, W).

Tetragonals and especially these in combination with octagonals cause domed shells.

2.3. METANEURALS

In old species the original number of metaneurals (= suprapygals) is three (figure 1, M, S). During the evolution of turtles this number is generally reduced by fusion of the metaneurals (figure 1, N-R,T-V). Most of the modern turtles have only two metaneurals (figure 1, I, J). Only few species have preserved their original number, which is considered as an atavism (figure 1, M). The general trend shows a reduction by fusion to a single metaneural plate, and the final stage is the fusion of the remaining metaneural with the pygal plate *Baena* (figure 1, L), *Eurysternum*.

Character code in this analysis: MN I, MN II "testudinids" = F, G, MN I, MN II "geochelonids" = H, I.

2.4. PYGAL PLATE

The pygal plate is the last element in the axial row of the carapace building the median part of the shell margin above the tail (figure 1, K). In some species this area is reduced by forming a caudal notch, as it can be observed in australochelyids, baenids and trionychins. With the former group most probably the metaneurals and the pygal plate are fused.

3. COMPARISON

Plate 1 to 3 shows the emydid (4/6/6/6) and testudinid (4/8/4/8) stucture at the same side positioned to the original row (6P/6P/6P/6P). Starting point always has to be the posterior median side of the nuchal plate, which is commonly concave in shape (figure 1, A). From this side in the very first turtles follows the hexagonal plate 6P (figure 1, 6). Such an orientation is seen in all following hexagonals up to the metaneurals. With few exceptions (Baenids, figure 1, L) this is the most common type of the neural row from the beginning of turtles to the Paleogene. Until the early Tertiary period the N I is formed more and more by a tetragonal plate especially in Chelydrids, Emydids, and Testudinids. As a result of the convex situation of the tetragonal plate (figure 1, 4), only a hexagonal plate 6A (figure 1, C) can insert in their posterior side. From now on the orientation of the following row is inverse. The tetragonal plate always act as a reversal (figure 1, B-4-C). The next reversal in the same row only can follow by an insertion of an octagonal plate which always is acting as a reversal (figure 1, C-8-follow). Tetragonal or octagonal plates never can be linked together, in any case they need a corresponding insertion plate. The same is true with the hexagonal plate 6P which can not follow a tetragonal or hexagonal plate 6A linked with an octagonal plate. It is evident that a multiple change in the orientation of the hexagonals needs an intercalation of tetragonals and octagonals (figure 1, B-4-C-8-follows). The most progressive type according to this rule shows the complete substitution of the hexagonals by both types of reversals within the Testudinids (4/8/4/8/4/8/4).

```
+---6P/6P/6P/6P/6P/6P/6P/6P/H/I
|
|                        +---4/8/4/8/4/8/4/8/H/I
|                        |
|                        |                        +---4/6B/6B/6B/6B/6B/6B/6B/H/I
1------------------------2------------------------4
|                        |                        +---4/6B/6B/6B/6B/6B/6B/6B/F/G
|                        |
|                        +---4/8/4/8/4/8/4/8/F/G
|                        |
|                        |                        +---4/6A/6A/6A/6A/6A/6A/6A/H/I
|                        +------------------------3
|                                                 +---4/6A/6A/6A/6A/6A/6A/6A/f/G
|
+---6P/6P/6P/6P/6P/6P/6P/6P/F/G [BASIC STAGE]
```

Tree 1.

```
+--6P/6P/6P/6P/6P/6P/6P/6P/H/I
|
|                +--4/8/4/8/4/8/4/8/H/I
|                |
1----------------2--4/8/4/8/4/8/4/8/F/G
|                |
|                |                +--4/6B/6B/6B/6B/6B/6B/6B/H/I
|                |                |
|                +----------------3--4/6B/6B/6B/6B/6B/6B/6B/F/G
|                                 |
|                                 |                +--4/6A/6A/6A/6A/6A/6A/6A/H/I
|                                 +----------------4
|                                                  +--4/6A/6A/6A/6A/6A/6A/6A/f/G
|
+--6P/6P/6P/6P/6P/6P/6P/6P/F/G [BASIC STAGE]
```

Tree 2.

4. PHYLOGENETIC RECONSTRUCTION

The phylogenetic analysis with PARS* shows the following relation:

(*Discrete character parsimony algorithm, version 3.6a3, written by Joseph Felsenstein. Copyright 1986-2000 by the University of Washington).

Both trees show the basic position (step one) of the "geoemydid type" of the neural row, in contrary to the more distant related "emydid type" (step three or four). The "geochelonid type" (step two) is closely related to the basic "geoemydid type". The importance of the metaneural character in turtles is subordinate to the neural characters (20% by number).

5. RESULTS

Finally the structure of the neural plate is variable (Pritchard, 1988) and can not be used as a taxonomic feature alone. Since the Cretaceous/Tertiary boundary the batagurines and testudins show the tendency of an increasing combinations with tetragonals and octagonals in respect to the more primitive species where hexagonals and tetragonals occur. The development of the dome shelled turtles (4/8/4/8/4/8/4) (figure 1, X) may be correlated with a drastic environmental change. Due to the cooling event during this time a domed shell is more capable to collect sun rays than a flat one. On the other hand some freshwater turtles e.g. *Kachuga, Graptemys* or *Tropidemys* show carinate shells with hexagonal plates. An extreme form is presented by the genus *Tropidemys* where a neural row of 6B is developed. This species is living in deep rivers, in a cool biotope, therfore its dome shaped shell is better adapted to collect sun rays than a flat shell could do.

Based on the parsimony character and neighboring analyses this study gives the proove that the neural formula 6P/ 6P/ 6P/ 6P/ 6P/ 6P/ 6P/ 6P/ must be the most primitive in turtles. Both variants (6P/6P/6P/6P/6P/6P/6P/6P/F/G [BASIC STAGE] and 6P/6P/6P/6P/6P/6P/6P/6P/H/I) only differ in the metaneurals.

ACKNOWLEDGEMENTS

We are greatful to James Ford Parham (University of California Berkeley) and to Walter G. Joyce (Yale Peabody Museum New Haven) for reading and commenting the script of this work and to Lisa A. Staley (Vancouver, Whashington) to correct the English version.

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