Festschrift for Marian Młynarski

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A survey of neural bone variation among recent chelonian species, with functional interpretations

Studia nad zmiennością neuraliów u współczesnych żółwi wraz z interpretacją funkcjonalną

Abstract. Neural bones are by far the most variable elements of the turtle shell. The presumed ancestral condition of about eight predominantly hexagonal neurals, each of which has the broad end anteriorly directed, may be modified in many ways — by proliferation of elements (to as many as fifteen); by reduction (usually at the ends of the series), with total loss of neurals in the extreme condition; and by changing in shape, by broadening, narrowing, reduction to isolated kite-shaped elements, reversal (to hexagons with the broad end posteriorly directed), or to an alternating arrangement of octagonal and quadrilateral elements. The literature reflects many of these variants, although in an incomplete and often anecdotal fashion, but records almost no attempts to hypothesize functional interpretations for the different neural bone configurations found among living turtles. In this paper, each of the major discrete neural configurations is correlated with other aspects of the anatomy, or with the behavior, of the species concerned.

I. INTRODUCTION

The turtle shell is a remarkable and biologically unique structure. Originally it presumably evolved as defensive armor in a relatively slow-moving early reptile, by means of anatomical modifications described by ZANGERL (1969). Subsequently it has been refined in many divergent ways in the course of evolution, by addition or subtraction of individual elements, by alterations in the thickness of the bone and the shape of the plastron and convexity of the carapace, and by the independent appearance of kinesis, especially in the plastron, in numerous chelonian lineages.

The gross morphology of the shell — its relative width and height, thickness, form of the plastron, and so on — has been discussed in considerable detail in the literature describing individual species. Additionally, the arrangement of, and variation in, the scutes covering the shell has an extensive literature (see e. g. GADOW (1899), PARKER (1901), NEWMAN (1906), COKER (1910), and ZANGERL (1969)). The overall architecture of the bony shell and its relationships to the muscles attached to it has received some recent attention in some important papers by Dennis BRAMBLE and his co-workers (BRAMBLE, 1974; BRAMBLE

and HUTCHISON, 1981; BRAMBLE, HUTCHISON, and LEGLER, 1984), but these papers discussed shell mechanics in terms of forces between individual non--kinetic elements only, without investigating forces between individual bones within the carapace.

Configurations and variations in the shell bones of living turtles have been very unevenly documented. Paleontologists, of course, have described the shell bones of most known species of fossil turtle, such elements often constituting the only material available; but they are constantly confounded in their attempts to make comparisons with living taxa, largely because the vast majority of museum specimens of modern species are liquid-preserved, with the shell bones concealed by the scutes, and the literature, doubtless for the same reason, is frustratingly incomplete.

Of the various bony elements of the turtle shell, some show little variation throughout the Order. Nearly all living turtles have four paired plastral bones and a single unpaired element (pelomedusids have five paired elements, whilst kinosternines lack the unpaired entoplastron). All turtles have a nuchal bone, and nearly all have eight pairs of pleural bones. Peripheral bones may show minor reduction in kinosternids, or even complete eliminations in most trionychids. But it is the median elements of the carapace — the neurals and suprapygals — in which extreme variation occurs.

BOULENGER (1889) recognized this variation and incorporated neural configuration in some of his generic definitions, and this approach was followed by such regional reviewers as SMITH (1931) and BOURRET (1941). These authors also illustrated the shell bones of numerous species, but BOULENGER'S excellent illustrations unfortunately led to a "typological" approach by many subsequent workers, who assumed that the turtles figured by BOULENGER could be considered typical of all individuals of the species shown — or even the genus. In fact, BOULENGER in many cases used specimens with rare or aberrant neural configurations (see examples below), and he made no attempt to investigate neural variation within species. Lack of curiosity on this point by subsequent authorities has resulted in some surprising statements in the modern literature, e. g. "On the whole, the bony mosaic of the shell is highly stable phylogenetically, and reduction of elements from or additions of them to the pattern illustrated... are notably rare" (ZANGERL, 1969), or "all the neurals are generally hexagonal, with the broad end facing anteriorly in the emydid turtles." (AUFFENBERG, 1976).

In recent years, there has been an awakening of interest in neural bone variation in living turtle species. The common belief that Australasian chelids uniformly lacked neural bones was significantly altered by the studies of BURBIDGE et al. (1974) and RHODIN and MITTERMEIER (1977), and the recent studies of BROADLEY (1981, 1983) have yielded valuable data on neural bone configuration in African pelomedusids and in *Kinixys*. PRITCHARD and TREBBAU (1984) gave data on neural bones in many Venezuelan turtle species, WEBB (1962) and MEYLAN (1984) studied neural variation in trionychids, and BOUR

(1981) documented neural configuration in some of the smaller testudinid genera. Yet the gaps that remain are surprising. North American turtles are in most respects the best studied in the world, yet, apart from *Trionyx* and *Gopherus* (documented by WEBB, 1962, and AUFFENBERG, 1976, respectively), data on the neural bones of turtles from that continent are anecdotal or non--existent, apart from occasional notes such as that of DOBIE (1981).

Furthermore, the literature is almost devoid of attempts to relate neural configuration to architectural advantage or behavioral adaptation. AUFFEN-BERG (1976) suggested that the alternating wider and narrow pleural bones of testudinids "apparently strengthens the dome", and BROADLEY (1981) wrote, in regards to neural loss in pleurodires: "There appears to be a tendency to strengthen the carapace by reduction of neurals from both ends of the series until they are completely eliminated and all costals makes median contact", but that is about as far as anyone has gone. Published accounts of neural configuration have generally been purely descriptive, making no attempt to assess reasons for the differences, and indeed implying that the differences, whilst sometimes diagnostic in generic or specific identification, are functionally meaningless.

It was with the intention of remedying these deficiencies of both information and interpretation that I examined turtle skeletons in my private colllection (specimens identified by the prefix PCHP), compared these with information in the literature, and attempted to rationalize the configurations found in terms of ecological or mechanical advantage. I am aware that systematic analyses of museum specimens would have greatly amplified series of most species. Nevertheless, some data are provided for all turtle genera, and for nearly all at least the modal condition is evident from the data provided, although information on intraspecific variation can only be deduced for those species for which the more extensive series of specimens were available.

Recent taxa only were studied. Nearly all the major configurations known in fossil species are represented among living ones; and it is usually very difficult to ascertain the full range of neural variation, or even the modal condition, for fossil taxa, among which the concept of a species is purely judgemental and the available material often very limited.

In describing neural configurations, I give a series of numbers corresponding to the numbers of faces or sides shown by each neural element, from front to rear. A designation such as 6A means that the element in question is hexagonal with the short sides (or the broader end) anteriorly, and 6P is the reverse. Designations such as 5A or 7A indicate that the element is asymmetrical and has one more short side anteriorly than posteriorly, 7P or 5P implying the reverse. A designation of an odd number (3, 5, or 7) without letter suffix indicates that the element is symmetrical; such elements only occur adjacent to contiguous pairs of pleural bones.

The first section of this paper summarizes the neural configurations in Recent chelonian genera. Subsequently, the main variant neural conditions

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or tendencies found in the Order are inventoried, and possible functional interpretations of these configurations pretented.

Abbreviations of museums: BM(NH) — British Museum (Natural History), London; BPBM — Bernice P. Bishop Museum, Honolulu; CDRS — Charles Darwin Research Station, Santa Cruz (Galapagos); FMNH — Field Museum of Natural History, Chicago; MLS — Museo del Instituto de la Salle. Bogota; MNHNP — Museum national d'Histoire Naturelle, Paris; PCHP — P.C.H. PRITCHARD private collection; UF/FSM — University of Florida, Florida State Museum, Gainesville; USF — University of South Florida, Tampa; USNM — National Museum of Natural History, Washington.

II. DESCRIPTION

Testudinidae

Aldabrachelys

The voluminous literature on this taxon includes little discussion of the neural configuration, beyond the statement by LOVERIDGE and WILLIAMS (1927) that the anterior neurals are typically octagonal and quadrilateral. In two specimens of *A. elephantina* examined, configurations of 4–8–4–8–4–5–7–6A and of 4–8–4–6–6–4–6 were recorded. Some fusion of elements had occurred in the latter, so earlier in life the specimens may have had more than seven neurals. BOUR (1984) illustrated the bony shell of *A. grandidieri*, with configuration 4–8–4–8–4–6–6–4–6A.

Specimens examined: *A. elephantina*: UF/FSM 62878, 62879.

Chersina

LOVERIDGE and WILLIAMS (1957) described the neurals in this genus as "... variable, approaching the octagonal and quadrilateral pattern", and illustrated a specimen with configuration 5P–7A–4–8–4–8–6. MEYLAN and AUFFENBERG (1986) found an anterior configuration of 4–8–4–8– to be typical for *Chersina*; all 24 specimens they examined (in the UF/FSM collection) had at least one octagonal neural; nearly all had at least two, and some had three.

Cylindraspis

This genus is now extinct, and, as shown in the fine engravings of GÜNTHER (1877), the bones of the shell generally ankylosed so completelly in adults that no traces of the sutures remained. Indeed, no trace of any shell sutures could be discerned in the bony shells of four specimens of *C. peltastes* examined. However, in one specimen of *C. vosmaeri* (MNHNP A5222), a configuration of 6P–6P–4–8–4–6–4 could be discerned, and in another specimen of

this species (BM(NH) 71. 11. 1. 52), general ankylosis of the shell bones had taken place, but there was an apparently octagonal element under vertebral II (i.e. presumably Neural IV).

In the type specimen of *C. graii*, a configuration of 4–8–6P–6P–5P–7P–6 is discernible, the last of these being followed by four completely asymmetrical elements of very variable size. In the type specimen of *C. borbonica*, a configuration of 6P–6P–6P–6P–4–8–4–6 is present (BOUR, 1984).

Specimens examined: *C. vosmaeri*: MNHNP A5222; BM(NH) 71.11.1.52; *C. peltastes*: BM(NH) 76.11.1.53 to 76.11.1.56; *C. borbonica*: MNHNP 1978— 3000; *C. graii*; MNHNP 9374.

Geochelone

The alternating octagonal-quadrilateral neural configuration is characteristic of all species of this genus, and is indeed one of the generic diagnostic characters. LOVERIDGE and WILLIAMS (1957) included the species currently allocated to the genera *Manouria*, *Aldabrachelys*, *Cylindraspis*, and *Indotestudo* in this genus; we shall use it in a more restrictive sense (PRITCHARD and TREBBAU, 1984), to include just the Neotropical species (subgenus *Chelonoidis*), the larger African tortoises together with *G. elegans* and *G. platynota* (subgenus *Geochelone*), and the larger Malagasy species (subgenus *Asterochelys*).

Statistically significant data on variation are only available for w few of these species, but these show that variation from the 4–8–4–8–4 typical anterior neural configuration is frequent. The species also differ in the degree of differentiation of the neurals. In *G. chilensis*, for example, the octagonal neurals (when present) are not much larger than the quadrilateral ones, whereas in *G. pardalis* the octagonal neurals are exceptionally large, greatly exceeding the quadrilateral elements in both breadth and in overall size. Only one case was found of median contact between any of the pleural bones.

Four specimens of *G. pardalis* were examined. Each had eight neurals, but the configuration differed in each (6P–6P–5P–7P–4–6A–6A–6; 4–8–4––8–4–7A–5A–6A; 4–8–4–8–4–8–4–6A; 4–8–4–8–4–8–4–4).

DERANIYAGALA (1939) examined the neural configurations of six specimens of *G. elegans*. He found eight neurals in each. In three, the neurals had configuration 4–8–4–8–4–6–6–6, but in the other three, neural I was 6P in form, reducing neural II to 4 or 6P. In one of these neural III was octagonal, in one neural IV was octagonal, and in one neurals IV and VI were both octagonal.

BOURRET (1941) illustrated the carapace bones of a specimen of *G. radiata* (as *Testudo hypselonota*) with neural configuration 4–8–4–8–4–6A–6A–6A.

Five specimens of *G. chilensis* were examined. Neural counts were 7, 7, 8, 8, and 9, and all had different configurations: 4–8–4–8–4–8–6; 6P–5P–5A–7A––5A–6A–6A–6; 6P–6P–6P–6P–6P–4–6A–8 (nine pairs pleurals); 4–8–4–8–5P––5A–6A–4–6A (nine pairs pleurals); 4–8–4–8–4–6P–6.

Thirteen specimens of *G. nigra* were examined. These included representatives of several subspecies (*G. n. abingdoni*, *G. n. becki*, *G. n. guntheri*, *G. n.*

microphyes, G. n. porteri, and *G. n. vandenburghi*), as well as a few identified to species only.

A high degree of variability was found. Indeed, in only four of the thirteen were neurals II and IV both octagonal. Configurations found in three *G. n. porteri* included 4–8–4–8–6P–4–6A–6A; 5P–7P–5P–7P–4–6A–6A–6A; and 5P–7P–8–4–6A–6–6A. In the last of these, neural III was of extraordinary size (about 20 cm long, the carapace length being 110 cm). In three *G. n. vandenburghi,* configurations were: 4–8–4–8–4–6A–6A–6 (twice), and 4–8–6P–6P–4––6A–6A–4–6A. In a specimen of *G. n. microphyes,* configuration was 4–8–6P––6P–4–6A–6A–4–6A; in a *G. n. abingdoni,* 4–8–5P–7P–6P–6P–4–6A; and in a *G. n. guntheri,* 5P–7P–6P–6P–5P–5A–6–6. In three specimens of uncertain origin, configurations were 4–8–6P–6P–6P–4–6A–6A, 4–8–6P–6P–5P–5A–6A––6A, and 4–8–4–8–6P–4–6A–6A. Perhaps most noteworthy of all was a specimen of *G. n. becki* in which pleurals I had an extensive median line of contact, separating the nuchal from the first neural (i. e. neural II if neural I was construed as missing). Unfortunately, the subsequent part of the neural series could not be examined because vertebral scutes II to V were still in place on the specimen.

The South American species *G. denticulata* and *G. carbonaria* are the only members of the genus with a tendency towards a cylindrical (or even constricted) rather than domed body form and it is not surprising that the neural configuration typical of "domed" representatives of *Geochelone* (i. e. octagonal neurals at positions II and IV) was only shown by a bare majority of specimens examined (athough all of 13 *G. denticulata* and 37 of 41 *G. carbonaria* had at least one octagonal neural somewhere in the series).

The thirteen *G. denticulata* each had eight neurals (except in one case of obvious transverse fission of neural I). In eight cases both neurals II and IV were octagonal; in two neurals I and II were 6P–6P, and in two 5P–7P; and in one neurals IV and V were 6–6 instead of 8–4. In two cases neural VI was octagonal, and in two cases neural VII. The last three neurals were typically each 6A or 6, but 6–4–6, 8–4–6 (twice), 6–8–4 (twice), and 5–6–6 were also found.

The 41 *G. carbonaria* included 32 with eight neurals each, six with seven (not counting single, fragmentary, intercalated bones in two of these); and three had nine (one being an obvious case of transverse splitting of neural I). Seventeen specimens had asymmetrical (odd-sided) neurals somewhere in the series. Fourteen specimens had three octagonal neurals (II, IV, VI); eight had II and IV (only) octagonal; eight had IV (only) octagonal; three had IV and VI (only) octagonal; three had II (only) octagonal; and one had VI (only) octagonal. In almost all cases, octagonal neurals were flanked anteriorly and posteriorly by quadrilateral ones. In eleven specimens neurals I and II had configuration 6P–6P, but in only one case were neurals I to IV all of this shape.

Specimens examined: *G. carbonaria*: PCHP 291—293, 319, 795, 1257—1259, 1261—1263, 1267, 1267—1271, 1275, 1276, 1278—1280, 1322, 1404, 1489,

1490—1491, 1494, 1614, 1731, 1732, 1844—1847, 1911, 1974, 2210, three unnumbered. *G. chilensis*: PCHP 1833—1837; *G. denticulata*; PCHP 284, 290, 796, 893, 2108—2114, 2181, 2306. *G. n. abingdoni*: CDRS unnumbered; *G. n. becki*: CDRS unnumbered; *G. n. guntheri*: PCHP 7; *G. n. microphyses*: CDRS unnumbered; *G. n. porteri*: CDRS unnumbered; two field specimens; *G. n. vandenburghi*: PCHP 494, 1971, 2302; *G. n. ssp.*: CDRS, two unnumbered.; *G. pardalis babcocki*: PCHP 509, 2167, 2169, 2170.

Gopherus

Although the two living species of this genus have relatively flat shells, they retain the modal pattern of alternating pleural bone width and octagonal/tetragonal neurals typical of more domed species. On the other hand, variability is unusually high, possibly because there is no longer any functional advantage (or disadvantage) in the alternating octagonal/quadrilateral neural condition, and the interneural sutures often are almost continuous with the interpleural sutures. Overall size contrast between the octagonal and quadrilateral neurals is usually modest. AUFFENBERG (1976), in a sample (of unstated size) of *G. polyphemus*, found 47% had the anterior five neurals with configuration 4-8-4-8-4; 8% had 4-8-4-8-5; 8% 4-8-5-5-4; 8% 5-7-4-7-4; 13% 4-8-4-8-6A; 8% 4-8-6-4-6P; 8% 4-8-4-4-6P. The posterior neurals are normally 4 or 6A in shape.

The following neural configurations were found in the specimens examined: 4-6P-4-6P-4-4-6-6P; 5P-7P-6P-6P-6P-4-6A-6-A; 4-6A-8-6P-4-6-8-4; 4-8--4-8-6A-6A-6-4; 4-6P-5P-7P-4-6-6A-6A; 4-8-4-8-4-6A-6A-6P-4; 4-8-5P--7P-4-6-8-4.

Data are lacking on neural variation in the rare congener *G. flavomarginatus*-AUFFENBERG (1976), however, found that 66% of the *G. flavomarginatus* examined had some scute or shell bone abnormality, compared to 52% of *G. polyphemus*.

Specimens examined: *G. polyphemus*: PCHP 883, 884, 1562, 1613, 1650, 2304, unnumbered.

Homopus

LOVERIDGE and WILLIAMS (1957) characterized *Homopus* as having the anterior neurals hexagonal or quadrilateral (i. e. not differentiated into octagonal and quadrilateral elements), but no systematic analysis of neural configurations in this genus has been conducted. MEYLAN and AUFFENBERG (1986) examined four specimens of *Homopus*, finding no octagonal neurals and a predominance of hexagonal elements with occasional 5—7 combinations. BOUR (1981) reported the rare occurrence of an octagonal neural at position IV in this genus. Usually two suprapygals are present (sometimes one), and the pleurals are distinctly differentiated into distally wide and narrow elements.

Indotestudo

BOURRET (1941) illustrated the shell bones of a specimen of *I. elongata* with neural configuration 4–8–4–8–4–6–6–6A (with a small median element intercalated between neurals VII and VIII). In three specimens examined, one had an identical configuration to that of BOURRET's figures: one had 4–8––4–8–4–6A–8–4, and the third had 6P–6P–4–8–4–6–6–6–6 (with nine pairs of pleurals). In one specimen of *I. forsteni* examined, a configuration of 4–8–4––7A–5A–6–6–6–4 was present.

Specimens examined: *I. elongata*: PCHP 1296, 1787, 2369; *I. forsteni*: PCHP 2120.

Kinixys

The anterior neurals in this genus are generally described as hexagonal (LOVERIDGE and WILLIAMS, 1957), and BOULENGER (1889: 142) illustrated a specimen in which neurals I to V are 6P in shape, neural VI tetragonal, and neurals VII and VIII 6A. BROADLEY (1981) examined eleven specimens of *K. belliana*, finding a typical complement of eight neurals and two suprapygals, exceptions being one with neural VIII fused with the adjacent suprapygal; the type of *K. zuluensis* in which an extra half suprapygal was inserted between the standard ones; and a paratype of *K. australis* with nine neurals, three suprapygals, and nine pairs of pleurals. Specimens illustrated by BROADLEY included one of *K. natalensis* with the configuration 6P–6P–6P–6P–4–6–6A–6P; *K. b. belliana* with 6P–6P–5P–7A–4–8–4–6P (with a triangular insertion between the right side of the last two); and *K. b. spekii* with 6P–6P–6P–6P–6P–5P–5A–6.

MEYLAN and AUFFENBERG (1986) reported that "nearly all Recent *Kinixys* have 6–6–6–6... anterior neural series", and that most, but not all, variation took place posterior to the hinge (neurals VI to VIII). One Miocene specimen of *K. erosa* had an octagonal neural II, a feature these authors could not find duplicated among Recent specimens, but which is present in PCHP 2307.

Among specimens examined, the following configurations were found: *K. belliana*: 6P–6P–6P–6P–4–8–4–6P–4 (4 suprapygals); 6P–6P–6P–6P–4––6A–6A–6P (three suprapygals); *K. erosa*: 4–8–6P–6P–6P–6P–4–6 (two suprapygals).

Specimens examined: *K. belliana*: PCHP 485, 1214; *K. erosa*: PCHP 2307

Malacochersus

The carapacial bones are extraordinarily reduced in *Malacochersus*. They have been well described by PROCTER (1922). PROCTER found a series of eight neurals present, with alternation of octagonal and tetragonal elements from positions I to VI. The point of exceptional interest, however, is that the octagonal neurals are the odd-numbered ones rather than the even-numbered, and

they have become octagonal by reduction of the corners of the phylogenetically tetragonal neurals in these positions. Laterally these neurals suture with the odd-numbered pleural bones, and anteriorly and posteriorly they make contact with adjacent neural bones; but the "corners" have disappeared into the enormous paired fontanelles that flank the midline. The even-numbered neurals, on the other hand, although octagonal in most tortoises, have become widely separated from their corresponding pleurals, and have become reduced to narrow rectangles. Neural VII is broadly hexagonal — bone is much more continuous in the posterior part of the shell than in the areas between and anterior to neural and pleurals VI. The eighth neural is tetragonal, and considerably expanded posteriorly.

Variation in the specimens examined consisted principally of proliferation of elements posterior to neural VI, as many as four essentially tetragonal elements replacing the two observed by PROCTER.

Specimens examined: *M. tornieri*: PCHP 405, 1298, 1300.

Manouria

The literature offers little information on the neural configurations in *Manouria*. LOVERIDGE and WILLIAMS (1957), by including it in their genus *Geochelone* and listing it as not having hexagonal neurals, implied that it had alternating octagonal/tetragonal neural bones. BOURRET (1941) illustrated the carapacial bones of a specimen of *M. impressa* with neural configuration 4–4–8–4–8–6P– –6P–6–4. The octagonal elements were distinctly enlarged and each made contact with three pleurals on each side. Pleurals I were unusually long, and were separated by two tetragonal neurals as well as by the anterior section of neural III. The bony sutures cannot all be discerned in the photograph of the bony carapace in OBST (1982), but it appears that, although there is a strong differentiation between alternating neurals in the anterior part of the series, the enlarged elements are hexagonal rather than octagonal; many of the transverse interneural sutures are noteworthy for their extreme convexity or concavity.

OBST (1982) also illustrated the shell bones of *M. emys phayrei*. The pleural bones alternate markedly in shape, but although the neural series is somewhat irregular, no octagonal elements are present. The configuration is 4–4–6P–4– –6A–6A–6A–6A–4, with a marked tendency for interneural sutures to be virtually continuous with the interpleural sutures. This tendency was also apparent in UF/FSM 52644, a specimen of *M. e. phayrei* illustrated by CRUMLY (1984); in this specimen, the neurals were generally irregular in shape, but the overall configuration was 4–6P–6P–4–6A–6A–6A–6A–6, with neural I small and short, possibly representing just a suturally separated posterior section of the nuchal bone. Neurals II, III, and IV were distinctly elongate.

Psammobates

LOVERIDGE and WILLIAMS (1957) characterized this genus as having "the neural bones hexagonal or vaguely quadrate or irregular, never with the regular octagonal and quadrilateral pattern that is characteristic of all Recent tortoises outside the Ethiopian region". MEYLAN and AUFFENBERG (1986) examined six specimens, finding only one octagonal neural although most included asymmetrical 5—7 combinations. BOUR (1981) found no octagonal neurals in this genus, which on grounds of cranial and shell characters he found virtually inseparable from *Homopus*; BOUR did not consider the strikingly different patterns of carapacial pigmentation to be an adequate generic character.

Pyxis

BOULENGER (1889) described this genus as having alternately octagonal and tetragonal neurals, and VUILLEMIN and RABODOMIHAMINA (1968) illustrated a specimen with configuration 4–8–4–8–4–8–6P–4. BOUR (1981) observed that *Pyxis arachnoides* may have neurals II; II and IV; or II, IV, and VI octagonal, and illustrated the extreme variability of posterior neurals and suprapygals with five diverse examples. BOUR (1981) considered the form *Acinixys planicauda* to be congeneric with *Pyxis* even though he found no specimen with any octagonal neurals, and illustrated a specimen with anterior configuration 6P–6P–6P–6P–6P–4–6–6. BOUR also illustrated the extreme posterior neural and suprapygal variation with three examples. However, despite the absence of octagonal neurals in *planicauda*, the pleurals were quite strongly differentiated into alternately widened and narrowed elements (although not as strongly as in *P. arachnoides*, in which pleurals III, V, and VII are separated from the peripheral bones by expanded lower ends of the even-numbered pleurals).

Testudo

The neural bones of individual specimens of this familiar genus have been illustrated by many authors, but no statistical analysis has been undertaken. As reported by LOVERIDGE and WILLIAMS (1957), the alternating octagonal--quadrilateral pattern, at least of the anterior neurals, is standard for this genus; it differs from *Geochelone* in having either a single suprapygal bone or two suprapygals separated by a transverse rather than a strongly curved suture (as well as cranial differences).

Except in rare cases, the first four neurals in *Testudo* have configuration 4–8–4–8. There may or may not be another octagonal neural at position VI. OBST and MEUSEL (1978) illustrated the disarticulated carapace bones of a specimen of *T. graeca ibera* (inexplicably lining up the neurals in reverse order between the pleurals), in which only six neurals were present, the last two being somewhat elongate and with configuration 6P–6A. More commonly in this form (as in

PCHP 2215 and 2370) there are seven neurals (4–8–4–8–4–8–6P). LOVERIDGE and WILLIAMS (1957) illustrated a specimen of *T. kleinmanni* with configuration 4–8–4–8–4–6–6–4, and PCHP 477 is a *T. g. terrestris* with configuration 4–8–4–8–5P–7A–6. PCHP 2211 is a *T. marginata* with configuration 4–8–4––8–4–8–6P, with an oblique, highly asymmetrical suture between the two suprapygals. PCHP 1238 is a *T. horsfieldi* with configuration 4–8–4–8–4–8–6P. PROCTER (1922) illustrated the shell bones of a very young *T. horsfieldi* in which the connections between the even-numbered (ultimately octagonal) neurals are not yet established. PCHP 2371 is a *T. hermanni* with configuration 4–8––4–8–4–6–6–6P. Another (PCHP 2212) has 4–8–4–7A–5A–6–6–5, with narrow median contact between pleurals VIII, and a single suprapygal.

Specimens examined: *T. hermanni*: PCHP 2212, 2371; *T. horsfieldi*: PCHP 1238; *T. graeca ibera*: PCHP 2215, 2370; *T. g. terrestris*: PCHP 477; *T. marginata*: PCHP 2211.

Xerobates

AUFFENBERG (1976) studied skeletal variation (including neural bone configurations) in the two living species of this genus. Many variant anterior neural configurations were found in a sample (of unstated size) of *X. agassizi*, as follows: 4–8–4–8–4 (50%); 4–7–5–8–4 ($3^1/_2$%); 4–8–4–6P–6P ($3^1/_2$%); 4–8–5–7–4 ($3^1/_2$%); 4–8–5–5–4 ($3^1/_2$%); 4–8–6–5–5 ($3^1/_2$%); 4–8–6–4–5 ($3^1/_2$%); 4–6A–6A–4–8 ($3^1/_2$%); 6P–6P–6P–8–4 ($3^1/_2$%); 6P–5–6P–6P–4 ($3^1/_2$%); 4–8–4––6A–4 (7%); 5–6P–6P––5–6P ($3^1/_2$%); 4–6A–6A–5–6A ($3^1/_2$%); 4–6A–6A–4–6A ($3^1/_2$). (One can surmise that there was one specimen of each of the „$3^1/_2$%" conditions, giving a sample size of about 30).

AUFFENBERG found less variation in a sample (probably of 20 specimens) of *X. berlandieri*. Anterior neural configurations found were: 4–8–4–8–4 (70%); 4–7–4–7–5 (5%); 4–8–4–8–6A (10%); 4–8–4–6A–4 (5%); 6A–7–4–8–4 (5%); 4–5–6A–8–4 (5%).

One specimen of *X. agassizi* was examined. The configuration was 4–8–4––8–4–8–4–6A.

Seven specimens of *X. berlandieri* were examined. Configurations found were 4–8–4–8–4–8–4–6A; 4–8–4–8–4–6A–8–4; 4–8–4–8–4–4–6–6; 4–8–4–8–4–6A–7A––5A–4 (neural VIII longitudinally divided); 4–8–4–8–4–6A–6A–6P–4; 4–8–4––8–4–6–6A–6A; 4–8–4–8–4–6A–6A–6A.

Specimens examined: *X. agassizi*: PCHP 134; *X. berlandieri*: PCHP 135, 886, 887, 1231, 1236, 1237, 1438.

Emydidae — Batagurinae

Annamemys

No specimens were examined, but BOURRET (1941) illustrated the shell of "*A. merkleni*" (= *A. annamensis*) with a neural configuration of 4–6A–6A––6A–6A–6–6–6, the neurals becoming wider posteriorly and forming an unbroken series.

Batagur

There specimens were examined. In all three, the first six neuruls had configuration 4–6A–6A–6A–6A–6A. In on specimen, Neural VII was pentagonal and followed by median contact between pleurals VII; pleurals VIII were separated by the elongate anterior suprapygal. In the other two specimens, eight neurals were present in each, the configuration of the last two being 6A–6A and 6A–6 respectively. In all three, the neural bones became progressively shorter und wider towards the rear, and the suture between the two suprapygals was anteriorly strongly convex, as in many testudinids.

Specimens examined: BM(NH) 1065.5.6.5.; two unnumbered.

Callagur

Two specimens were examined. One had eight neurals, one nine; in both cases neural I was tetragonal and subsequent neurals (except for the last) 6A in form, the last neural being 6 in shape. The posterior suprapygal was larger than the anterior, with the suture between transverse or slightly convex anteriorly.

Specimens examined: BM(NH): 97.3.4.15, 97.3.4.16.

Chinemys

The neural bones of *Chinemys* are wide and form a continuous series, and are generally described as hexagonal and short-sided in front (i. e. 6A) in shape (e. g. SMITH, 1931). This was indeed found in a specimen of *C. reevesi* examined, except that neurals V and VI were 7A–5A instead of 6A–6A. Hexagonal-A neurals were also observed in a 20.2 cm specimen of *C. megalocephala* with a skull 5.2 cm wide, even though the majority of macrocephalic turtles have an octagonal neural towards the anterior part of the series. Perhaps *C. megalocephala* is not a valid species, but rather is based upon molluscivorous populations of *C. reevesi* in which ontogenetic enlargement of the head occurs.

Specimens examined: *C. reevesi*: PCHP 505; *C. megalocephala*; PCHP 2309.

Cistoclemmys

In two specimens of *C. galbinifrons* (PCHP 1936, 1939), six and seven neurals, respectively, were present, all being 6P except for the last which was pentagonal. In one, pleurals VII and VIII made median contact, and in the other only pleurals VIII. The latter configuration was illustrated by BOURRET (1941).

Two specimens of *C. flavomarginata* each had seven neurals (pleurals VIII in median contact); configurations were 6P–6P–6P–6P–6P–6P–5 and 4–8–6P–
–6P–6P–4–6A–5.

Specimens examined: *C. galbinifrons*: PCHP 1936, 1939; *C. flavomarginata*: PCHP 1384, 2023.

Cuora

BOULENGER (1889: 129) illustrated a specimen of *C. amboinensis* with seven 6P neurals, the last making contact with the upper suprapygal, so that all pleural pairs were separated medially. However, I was unable to find a similar configuration in any of the six specimens examined (two of the domed mainland form and four of the flatter Indonesian form), in all of which the first six neurals were of the 6P type, followed by a pentagonal element, and in all of which pleurals VIII made median contact, as was illustrated by BOURRET (1941: 149). In a single specimen of *C. trifasciata*, a different configuration was found: 4–8–6P–6P–6P–4–6A–5, with pleurals VIII in median contact, but none were in contact in the specimen illustrated by BOURRET (1941: 153).

Specimens examined: *C. amboinensis*: PCHP 127, 332, 2317, 2318, 2319, 2366; *C. trifasciata*: PCHP 315.

Cyclemys

In *Cyclemys dentata*, the neurals are moderately broad and form a continuous series, usually of seven. The anterior part of the series is composed of 6P elements, with a point of inflection to 6A elements reached by means of a square neural at position VI (n = 3) or V (n = 1). BOURRET (1941) illustrated a specimen with a tetragonal neural VI. The posteriormost neural may be distinctly elongate and with a dorsal vertebra attached to its anterior part only; such an element may well correspond to a composite of the posteriormost neural and the anterior suprapygal.

In a single specimen of *C. tcheponensis*, eight neurals were present (6P–6P––6P–6P–4–6A–6A–6A). BOURRET (1941) illustrated one with configuration 6P–6P–6P–6P–6P–6P–6P–4.

Specimens examined: *C. dentata*: PCHP 353, 1067, 1068, 1432; *C. tcheponensis*: PCHP 2061.

Geoclemys

In *Geoclemys hamiltoni*, the neurals are moderately broad, eight in number, and form a continvous series. Neural I is tetragonal and the subsequent neurals typically hexagonal-A. However, neural VIIII may be 6 rather than 6A in shape.

Specimens examined: PCHP 487, 488.

Geoemyda

In the single specimen of *G. spengleri* examined, the neural configuration was 6P–5P–7P–6P–6P–6P–4–6A. This is in keeping with the usual characterization of the *Geoemyda*-group ("hexagonal neurals nostly short-sided behind"), but no information on variability is available. BOURRET (1941: 155) illustrated one with configuration 6P–6P–6P–6P–6P–6P–6P–4.

Specimen examined: PCHP 2316.

Hardella

Two specimens of *Hardella thurji* were examined. In one, a configuration of 4–6A–6A–6A–6A–6A–6A–6 was present, followed by two suprapygals, the posterior one by far the larger. In another specimen the posterior part of the series could not be discerned, but the first six neurals had configuration 4–6A–6A–6A–6A–8.

Specimens examined: BM(NH) 87.3.36.6, unnumbered.

Heosemys

BOULENGER (1889) illustrated the neural configuration of a specimen of *H. grandis*. Seven rather broad neurals, all hexagonal-P in shape, were present in a continuous series. Two specimens examined differed in having an additional tetragonal neural intercalated between neurals VI and VII, and in having a third suprapygal, in one case anterior to the anterior "standard" suprapygal, and in the other inserted into the suture between the two suprapygals. In one of these specimens the two anterior neurals had configuration 4–8 instead of 6P–6P. BOURRET (1941) illustrated a specimen of *H. grandis* with configuration 4–8––6P–6P–6P–6P–4–6, with three suprapygals.

In four specimens of *H. spinosa*, the neurals were very wide, the first six being hexagonal-P and neural VII tetragonal, making contact laterally only with pleurals VII. The anterior suprapygal is typically elongate, completely separating pleurals VIII and partially separating pleurals VII. However, in two cases it was transversely divided, and in one case neural VII was hexagonal-P rather than tetragonal.

Specimens examined: *H. grandis*: PCHP 68, 1676. *H. spinosa*: PCHP 67, 1215, 1447, 1527.

Hieremys

In *Hieremys annandalii*, the neurals are moderately broad and form a continuous series. The neural configuration appears to be quite variable. In two specimens examined, configurations encountered were: 6P–6P–6P–6P–6P––6P–4–6A and 4–6A–5P–5P–6P–6P–6. In the latter specimen, the sutures separating neurals II to V were almost perfectly continuous with the corresponding interpleural sutures.

BOULENGER (1889: 108) illustrated a specimen with a configuration of 4–6A–8–6P–6P–6P–5P–5, and BOURRET (1941) illustrated one with configuration 4–8–6P–6P–6P–6P–6P–4. In two of the specimens described here, the upper suprapygal was transversely divided.

Specimens examined: PCHP 1418, 1446.

Kachuga

The neural configurations in this genus have been mentioned by BOU-LENGER (1889), SMITH (1931), BOURRET (1941), McDOWELL (1964), and others, but without any systematic analysis. Observations made by these authors include the summary "Neurals hexagonal, short-sided in front", and the curious anterior elongation of the fourth vertebral scute in the smaller species (*K. smithi*, *K. tecta*, *K. sylhetensis*), so that this scute covers parts of five neural bones. In the larger species such as *K. trivittata*, in which the shell is relatively low and with the streamlining typical of large river turtles, the anterior neurals (only) are narrowed and elongate.

SMITH (1931) reproduced BOULENGER's (1889: 133) illustration of the shell bones of *K. trivittata*, and BOURRET (1941) illustrated another specimen. The neurals form a continuous series of eight, neural I being tetragonal and the remainder 6A except that the suture behind neural IV and pleurals IV is virtually continuous, so that neural IV is (almost) octagonal, and neural V tetragonal. Neurals I to IV are very long and narrow, neural V intermediate, and neurals VI to VIII quite short.

In a specimen of *K. kachuga*, the neurals are hexagonal throughout the series, with the exception that the posterior part of neural VII is split off to give a narrow tetragonal element; again neural V is intermediate between the long anterior elements and the short posterior ones. In another specimen the carapace is incomplete, but the first six neurals (at least) were similar.

The neurals are quite different in the small species *K. tecta*. In four specimens examined, there was no elongation of the anterior neurals, but neurals III and especially IV were generally enlarged, the latter octagonal and bearing the high tubercle defining the posterior part of vertebral scute III. Otherwise, neurals II to VIII were hexagonal-A in shape, with the exception of the tetragonal neural V, and the exception of PCHP 2364, in which only seven neurals were present, the seventh 7A in shape.

An octagonal neural IV is sometimes present in members of the genus that do not show spectacular elevation of the dorsal tubercle on vertebral II; in two specimens of *K. kachuga* examined in the BM(NH) collection, one had configuration 8-4 for neurals IV and V, while the other had 6A neurals throughout the series (except for the tetragonal neural I). In four specimens of *K. smithi*, three had configuration 4-6A-6A-8-4-6A-6A-6A, and the fourth had an asymmetrical variant condition with neurals IV and V 7A-5A instead of 6A-6A.

Specimens examined: *K. kachuga*: PCHP 1466, 1467; BM(NH) 97.3.05, unnumbered; *K. smithi*: BM(NH) (four, unnumbered); *K. tecta*: PCHP 1469, 1471, 2364, 2365.

Malayemys

In *Malayemys subtrijuga,* the eight neurals are broad and form an unbroken series. The original condition probably consisted of a tetragonal neural I followed by seven hexagonal-A elements, but this condition was only encountered in one of six specimens examined. In two, neural I was altered to hexagonal-P by posterior suture displacement. There is also a tendency for octagonal neurals to form at position III and/or V, with consequent modification of intervening or following elements to a tetragonal shape. Octagonal neurals at both these positions were only seen in one specimen, but in another neural III was heptagonal-A and neural V octanogal.

SMITH (1931) illustrated a specimen with a 4–6A–8–6P–6P–4–6A–6A neural condition, and BOURRET (1941) one with 4–4–6A–6A–6A–6A–6A–6.

Specimens examined: PCHP 66, 1389, 1390, 1391, 1447, 1448.

Mauremys

The turtles of this genus were included in *Clemmys* until MCDOWELL (1964) divided that genus into *Clemmys, Mauremys,* and *Sacalia.* Authors such as SMITH (1931) and BOURRET (1941) describe the neurals as hexagonal and short-sided in front; both of these authors uncritically repeated the generic diagnosis of BOULENGER (1889), who illustrated a specimen of *M. leprosa* with a continuous series of relatively broad neurals, all but the first of which were 6-A is shape. However, MCDOWELL (1964) observed that *M. mutica* was quite variable in its neural configuration, a series of seven from Hainan including only three with the "typical" pattern, and the others having an octagonal neural in the series (at position II, III, and IV respectively), behind which the remainder of the hexagonal neurals were 6-P in shape.

In one specimen of *M. mutica* examined, neural I was tetragonal and neurals II to VII 6-A in shape, posteriorly contacting an elongate anterior suprapygal that completely separated pleurals VIII and partially separated pleurals VII. In another specimen, a completely different neural configuration (4–8–5P–7A–4––6A–6A–6A) was found. In a specimen of an undescribed form related to *M. mutica,* eight neurals were present, all being 6A except neurals I (tetragonal) and VIII (hexagonal-P).

A single specimen of *M. japonica* also showed irregular neurals, with configuration 4–6A–6A–8–6P–5P–5A–6.

Specimens examined: *M. mutica:* PCHP 1071, 2367; *M.* cf. *mutica:* PCHP 2314; *M. japonica:* PCHP 2368.

Melanochelys

BOULENGER (1889) illustrated a specimen of *Melanochelys trijuga* with a continuous series of relatively broad neurals with the configuration 4–8–6P––6P–4–6A–6A–6A. DERANIYAGALA (1939: 254) found eight neurals in each of

five specimens of *M. trijuga*, with configuration similar to that found by Bou-
LENGER except that in one specimen the tetragonal element occupied position
VI instead of position V.

Morenia

There is no recent primary literature on this genus. BOULENGER (1889: 67)
illustrated the shell bones of *M. ocellata*, showing a continuous series of relati-
vely broad neurals, seven in number, with configuration 4–6A–6A–6A–6A–6A–8.
This specimen and two others in the BM(NH) collection were examined. In
one a configuration of 4–6A–6A–6A–6A–6P–6 was present, and in the other
the posterior section was indiscernible but the first six neurals had configura-
tion 4–6A–6A–6A–6A–8. There thus may be a regular tendency towards the
formation of an octagonal neural towards the rear in this species. Neural VII
was separated from the broad lower suprapygal by a second, almost perfectly
rectangular suprapygal separating pleurals VIII. In a single (live) specimen
of *M. petersi* examined, the neural bones were clearly visible through
the vertebral scutes. The series was relatively broad and unbroken, with con-
figuration 4–6A–7A–5A–6A–6A–6A–5. There was only one suprapygal, and
even though the anterior part of the suture between pleurals VIII was penetra-
ted by the pentagonal neural V, posteriorly these bones had a broad median
contact.

Specimens examined: *M. ocellata*: BM(NH) 1887.3 11.7; two unnumbered;
M. petersi: one living.

Notochelys

As BRAMBLE (1974) observed, this genus is quite distinct from the other
batagurines with hinged plastra (*Pyxidea*, *Cuora*, *Cyclemys*, *Cistoclemmys*,
etc.), and this difference is also reflected in the neural bones, which in *Noto-
chelys* are generally hexagonal-A in shape. In the two specimens examined,
the tetragonal first neural was followed by a continuous, rather broad but
posteriorly narrowing, series of seven 6–A neurals.

Specimens examined: PCHP 1392, 2366.

Ocadia

BOULENGER (1889: 87) illustrated a specimen of *Ocadia sinensis* with a series
of eight moderately broad neurals forming a continuous series and with con-
figuration 4–6A–6A–6A–6A–6A–6A–6A. This is similar to that of the single
specimen examined. BOURRET (1941) illustrated a specimen with a single octa-
gonal element replacing neurals VII and VIII.

Specimen examined: PCHP 1086.

Orlitia

BOULENGER (1889) included *Orlitia borneensis*, together with *Siebenrockiella crassicollis*, in the genus *Bellia*, which he characterized as having "neural plates hexagonal, short-sided in front". Otherwise I have no information on the neural bones in this genus.

Pyxidea

The neural bones of *Pyxidea mouhoti* are similar to those of the related *Cyclemys dentata*, except that they are considerably broader, possibly correlated with the more arched or elevated carapace. BOURRET (1941) illustrated a specimen with configuration 6P–6P–6P–6P–6P–4–6A–6.

Specimen examined: PCHP 2373.

Rhinoclemmys

Statements in the literature about neural bone configurations in this genus (McDOWELL, 1964; ERNST, 1978) tend to be oversimplified, usually referring just to the hexagonal-P condition of the neural bones. However, PRITCHARD and TREBBAU (1984) provided a more detailed and accurate discussion.

The typical neural configuration in *Rhinoclemmys* is 6P–6P–6P–6P–6P––4–6A–6A, but this is not shared by all species, and is also highly variable within species. The eight element is often elongate and with an attachment area for a dorsal vertebra only on the anterior part of the visceral face, and this may represent a composite between neural VIII and the first suprapygal. Neural II is sometimes octagonal (in two of seven *R. diademata*; five of seven *R. punctularia*; five of eighth *R. melanosterna*; and three of four *R. funerea*), in which case neural I is tetragonal rather than hexagonal (in one *R. funerea* the anterior two neurals had a 5P–7P configuration). In one *R. melanosterna* neural V was octagonal also. Neural VII was octagonal in one of two *R. nasuta*. The neural series normally includes eight elements, but only seven were present in one of seven *R. punctularia*, five of eleven *R. pulcherrima incisa*, and all of three *R. p. manni*. The tetragonal element at position VI was shifted to position VII in one of the *R. diademata*, two of the *R. punctularia*, and five of the *R. melanosterna*, and to position V in one of the *R. p. incisa* and one of four *R. annulata*. The tetragonal element was also quite frequently distorted to a pentagonal configuration by oblique interneural sutures (total of ten specimens of all species).

Apart from a single *R. annulata* with configuration 8–6P–4–8–4–6–6–4, the most deviant configurations were found in the three *R. rubida perixantha* examined. In two of these there was median contact between pleurals VIII (and very narrow contact between pleurals VII in one of these), and in both of these specimens a narrow, oval element was inserted into the suture between

pleurals VIII — either isolated or contiguous with the suprapygal. Actual configurations in these specimens were: 6P–6P–6P–5P–7P–4–6A–5; 6P–6P––6P–5P–5A–6A–5; and 6P–6P–6P–5P–7P–4–6A–6A. The anterior neurals showed alternation in length, I and II being long and III and IV rather short.

PRITCHARD and TREBBAU (1984) observed an almost symmetrical pair of supernumerary bones inserted between the nuchal bone and pleurals I in three of ten specimens of *R. pulcherrima* examined, and a unilateral insertion of this kind in one other specimen.

Specimens examined: *R. diademata*: PCHP 1228, 1339, 1475—1477, 1516, 1517; *R. punctularia*: PCHP 296, 345, 502, 796, 882, 1813, 1838; *R. funerea*: PCHP 348, 1126, 1127, 1730; *R. annulata*: PCHP 48, 49, 1132, 1222; *R. rubida perixantha*: PCHP 1234; USF 290, 291; *R. pulcherrima incisa*: PCHP 295, 880, 1087, 1208, 1444, 1453, 1483, 1839, three unnumbered; *R. p. manni*: PCHP 181, 2153, 2154; *R. p. rogerbarbouri*: PCHP 207, 208; *R. melanosterna*: PCHP 2432—2440; *R. nasuta*: PCHP 2442, 2443.

Siebenrockiella

The neural configuration shown by BOULENGER (1889: 99) and by BOURRET (1941: 166) is typical, i. e. seven relatively wide neurals with configuration 4–6A–6A–6A–6A–6A–6A, with no median contact between any of the pleurals. Minor variations observed in the series of six specimens included one in which the large anterior suprapygal failed to make contact with the posteromedian corners of pleurals VII, and one in which neurals IV and V had a displaced suture, giving a configuration of 7A–5A instead of 6A–6A.

Specimens examined: PCHP 11, 12, 1445, 1486, 1486, 2140, 2141.

Sacalia

In both specimens of *Sacalia bealei* examined, seven rather broad neurals, forming a continuous series, were present; neural I was tetragonal and the remainder hexagonal-A in shape. The anterior suprapygal was somewhat elongate, completely separating pleurals VIII and making narrow contact with pleurals VII. BOURRET (1941: 170) illustrated a similar configuration (under *Clemmys quadriocellata*).

Specimen examined: PCHP 2364, 2619.

Emydidae — Emydinae

Chrysemys

In *Chrysemys picta*, the neural bones form a continuous series from the nuchal bone to the suprapygals. Usually there are eight neurals, neural I being tetragonal and the remainder hexagonal-A in shape, becoming broader and shorter

towards the rear. In one specimen, the last two neurals had configuration 7A–5A instead of 6A–6A.

Specimens examined: *Chrysemys p. picta*: PCHP 182, 1420; *C. p. bellii*: PCHP 333; *C. p. marginata*: PCHP 1401.

Clemmys

Three specimens of *Clemmys insculpta* were examined. The neural series was of moderate and essentially constant breath. In two it comprised eight elements forming a continuous series from the nuchal bone to the suprapygal. Neurals were uniformly hexagonal-A in shape except for the tetragonal first element. In the third specimen, neural VIII was fused with the anterior supracaudal, leaving only seven distinct neurals, and neurals I to II were 5P–5A instead of 4–6A. In both adults, neural III was elongated and VI and VII shortened; the difference was less evident in the subadult.

In a specimen of *C. marmorata*, neural I was tetragonal and neurals II to VII hexagonal-A in shape; three small tetragonal elements separated neural VII from the enlarged suprapygal.

In *C. guttata*, configurations of 4–6A–6A–6A–6A–6A–6A–4 were found in both specimens examined.

Specimens examined: *C. insculpta*: PCHP 1177, 1223, 2013; *C. marmorata*: PCHP 64; *C. guttata*: PCHP 1200, 1450.

Deirochelys

In *Deirochelys reticularia*, the (usually eight) neurals are broader than in any other emydine (except possibly *Emydoidea*), and form a continuous series. Except for the tetragonal neural I, all the neurals are normally hexagonal. In the anterior part of the series (II to V at least), the neurals are hexagonal-A; however, posteriorly 6 or 6P neurals may be present. In one specimen an additional tetragonal element was inserted between neurals VII and VIII.

Specimens examined: PCHP 172, 173, 1069, 1431, unnumbered.

Emydoidea

In *Emydoidea blandingii*, the neurals are very broad and seven in number. Neural I is tetragonal and neural II usually octagonal. The remainder of the series usually consists of a tetragonal and a series of hexagonal elements, usually 6A in shape but the terminal element may be 6. Asymmetrical sutural displacement (e. g. to 4–7A–5A–7A–5A–6A–6 or to 4–8–4–7A–5A–6A–6) may occur. The large anterior suprapygal separates pleurals VIII and partially separates pleurals VII.

Specimens examined: PCHP 307, 1179, 1180.

Emys

BOULENGER (1889: 111) illustrated a specimen of *Emys orbicularis* with neural configuration 4–6A–6A–6A–6A–6A–6A–6, the neurals forming a continuous series of moderate breadth. MŁYNARSKI (1976) illustrated a similar configuration. In the specimens examined, one had seven neurals and an elongate anterior suprapygal that separated pleurals VIII and partially separated pleurals VII, and the other had eight neurals but with an anterior configuration of 4–7P–5A.

Specimens examined: PCHP 1458, 2022.

Graptemys

Typically eight neurals are present, the first tetragonal, the next six hexagonal-A, and the eighth 6A or 6P. Such a condition was found, for example, in nine specimens of *G. barbouri*, as well as in individul specimens of *G. flavimaculata* and *G. geographica*. A second specimen of *G. flavimaculata* had neurals II and III with configuration 8—4 insted of 6A–6A.

The most distinctive configurations are found in *G. pulchra*. In four specimens from the Conecuh River (Alabama/Florida) examined, only one had the typical generic configuration. In the other three, only seven neurals were present, the seventh being octagonal; and in one of these, neurals I to III had configuration 5P–7P–4 instead of 4–6A–6A. DOBIE (1981) considered the presence of only seven neurals to be a peculiar characteristic of the Conecuh River population of *G. pulchra*.

Suprapygals were quite variable, being one to three in number.

Specimens examined: *G. barbouri*: PCHP 26, 27, 286, 1070, 1452, 1587, 1588, 1704; *G. pulchra*: PCHP 29, 84—86; *G. flavimaculata*: PCHP 806, 1556; *G. geographica*: PCHP 1776.

Malaclemys

In *Malaclemys* terrapin, the neurals form a moderately broad and continuous series from the nuchal bone to the (variable) suprapygals. The modal configuration is 4–8–4–6A–6A–6A–6A, generally followed by one to a few very small or fragmentary bones between neural VII and the anteriormost suprapygal. Neural IV may also be octagonal (three out of thirteen), or heptagonal (two out of thirteen). When neural IV is octagonal, it is followed by a tetragonal or hexagonal-P element. Neural II was octagonal in 11 of 13 specimens, and heptagonal in one other; in one specimen, the configuration was 4–6A–6A––6A–6A–6A–6A–(fragments).

DOBIE (1981) illustrated *Malaclemys* neural bones that included octagonal elements at positions II and VII, but without comment except to note that neural VIII in this genus usually makes contact only with pleurals VIII (cf

Graptemys, in which neural VIII is usually hexagonal, contacting pleurals VII and VIII).

Specimens examined: *M. t. terrapin*: PCHP 1563, 1564; *M. t. centrata*: PCHP 309—311; *M. t. tequesta*: 335, 1199, 1625; *M. t. rhizophorarum*: PCHP 1555, 1562, unnumbered; *M. t. macrospilota*: PCHP 1481, unnumbered.

Pseudemys

PRITCHARD and TREBBAU (1984) discuss neural bone variation in this genuss The usual configuration is one of eight neurals, forming a continuous serier decreasing in breadth posteriorly, with neural I tetragonal and the remainde-hexagonal-A in shape. Eighty-seven carapaces representing 17 taxa were exa. mined. Variants from the typical generic configuration included:

Anterior configuration 5P–5A was found in one specimen of each of *P. f. floridana*, *P. f. peninsularis*, and *P. s. elegans*.

Anterior configuration of 6P–4 was found in one specimen of each of *P. dorbigni*, *P. terrapen*, and *Pseudemys* sp. incert.

Anterior configuration of 4–6P–4 was found in one specimen of *P. s. callirostris*.

A series of seventeen *P. s. chichiriviche* showed a high degree of variation in neural II; this element was 6A in three specimens; 6P in two; asymmetrically hexagonal (contacting pleural II only on the left, but pleurals I, II, and III on the right); heptagonal in three; pentagonal in two; and octagonal in six.

There is some variation in overall width of the neural series through the genus, the neurals tending to be wider in pond-dwelling forms such as *P. s. scripta* and narrower in larger riverine forms such as *P. f. peninsularis*. However, overlap occurs. Medially contiguous pleurals are very rare in *Pseudemys*. However, a narrow connection between pleurals VIII was evident in an adult *P. c. suwanniensis* (PCHP 1386).

Although the neural bones are not characteristically differentiated in *Pseudemys* as they are in testudinids, the pleural bones are notably differentiated, odd-numbered elements being distally much broader than even-numbered ones.

Specimens examined: *P. dorbigni*: USNM unnumbered; *P. s scripta*: PCHP 303—306, 320, 321; *P. s. callirostris*: UF/FSM unnumbered; PCHP 1528—1531, 1539; *P. s. cataspila*: PCHP 912, 1084, 1085, 1244—1252; *P. s. chichiriviche*: PCHP 1464—1472; 1520—1525; UF/FSM 53333, 53334; *P. s elegans*: PCHP 299—302; *P. s. nebulosa*: PCHP 403, 404; *P. f. floridana*: PCHP 1130, 1164; *P. f. peninsularis*: PCHP 492, 493, 911, 916, 917, 1121, 1138, 1147, 1156, 1157, 1159, 1160, 1183, 1184, 1317, 1624, 1702; *P. c. suwanniensis*: PCHP 1386, 1402; *P. nelsoni*: PCHP 101, 298, 1120, 1133, 1293, 1385, 1440, 1703, 1951; *P. rubriventris*: PCHP 1430; *P. terrapen*: PCHP 1319; *P. decorata*: PCHP 334; *P. stejnegeri*: PCHP 1318; *P. alabamensis*: PCHP 99; *P.* sp. incert (Ponce de Leon, Florida): PCHP 352.

Terrapene

This genus is abundant in North America and is well represented in museum collections. Nevertheless, although the genus has had several important chroniclers (e. g. MILSTEAD, 1969), no analysis of neural variation appears in the literature. A partial explanation for this dearth of information lies in the fact that most museum specimens of *Terrapene* are fluid-preserved or dry preparations with scutes intact and shell bones inaccessible, and the bony preparations that do exist are for the most part those of adults, in which general shell ankylosis typically occurs so that neurals are not discernible.

Nevertheless, BOULENGER (1889: 116) illustrated the neural configuration of a specimen of *T. carolina,* and (for once) the pattern shows is reasonably typical of the genus. Most commonly, the neurals are hexagonal-A in shape, and with median contact between pleurals VIII, but variation from this is frequent and well worthy of further study.

Configurations encountered in five specimens of *T. carolina bauri* were as follows: 4–8–4–6A–6A–7 (pleurals VIII in contact); 4–6A–6A–6A–6A–8 (pleural pairs VII and VIII in contact); 4–6A–6A–6A–6A–6A–6A (pleurals VIII in contact); 4–7P–5A–6A–6A–7A–4 (pleurals VII in median contact but partially separated by an isolated small neural; pleurals VIII completely separated by an additional suprapygal); 4–8–4–7P–5A–6A–7 (pleurals VIII in median contact). In the majority of specimens examined (not listed below), including some of quite small size, general shell ankylosis was complete and no sutures could be discerned. On the other hand sutures were quite distinct in the last specimen above, even though it is the largest known representative of this subspecies.

In three specimens of *T. c. carolina,* six, seven, and eight neurals, respectively, were present. The first five bones were always 4–6A–6A–6A–6A, subsequent to which configurations of 7 (pleurals VII and VIII in contact); 7A–6A (pleurals VIII in contact); and 6A–7P–5 (pleurals VIII in contact) were found.

In two specimens of *T. c. major,* anterior configurations of 4–6A–6A–6A–6A were also recorded, followed by 6A–5 and 7P–4A respectively (in both, pleurals VII and VIII had median contact).

Seven bony shells of *T. c. mexicana* were examined carefully but to sutures could be distinguished. Neural sutures were also obsolete in a large specimen of *T. n. nelsoni,* but were clear in another, in which an anterior configuration of 4–8–4–8–4 was observed. In *T. ornata,* a species related to *T. nelsoni,* such a configuration may also occur, although in the specimen examined it was distorted slightly (4–8–5P–7P–4–6A–6A–5; pleurals VIII in contact).

Specimens examined: *T. c. carolina:* PCHP 1400, 2110, 2014; *T. c. bauri:* 117, 1170, 1440, 1485, 1816; *T. c. major:* PCHP 126, 1174; *T. c. mexicana:* PCHP 1181, 1182, 1242, 1393, 1394, 1434, 2023; *T. o. ornata:* PCHP 2365; *T. nelsoni:* PCHP 1842; UF/FSM 27138.

Chelydridae

Chelydra

It is surprising that even recent authors illustrating or discussing the neural bones of this common taxon (e. g. MŁYNARSKI, 1969; ERNST, GIBBONS and NOVAK, 1985) apparently based their information upon an illustration provided by BOULENGER (1889: 22), although the specimen illustrated more recently by ZANGERL (1939: 396) was much more typical. In BOULENGER's illustration of *C. serpentina*, neurals II to VII are all hexagonal-A, followed by two suprapygals and a pygal. I was unable to find such a configuration among eighteen specimens representing all four subspecies (although mostly *C. s. osceola*). The closest approach was PCHP 2363 (*C. s. osceola*), in which nine neurals were present, with configuration 4–6A–6A–6A–6A–6A–6P–6P–4. Among the series of eighteen, nine neurals were usually present (n = 13), three had eight, and two had ten. However, in some cases there is a potential for ambiguity in differentiating the last neural from the first suprapygal, and in one specimen with ten neurals, one of the interneural sutures was very poorly defined.

Despite the absence of octagonal neurals in BOULENGER's illustration, we found a very high frequency of specimens with one or more octagonal neurals. In 13 cases, neural II was octagonal; it was heptagonal in two others, this presumably being a unilateral modification of the octagonal condition; and hexagonal in only two. The tendency towards alternating octagonal and tetragonal elements at the anterior part of the series, typical of many testudinids, was also quite marked; in eight specimens (as well as in ZANGERL's illustration), neurals II and IV were octagonal, in one neurals II, IV, and VI were all octagonal, and in single specimens neurals II and VI, and II and VII, were octagonal. In one specimen with nine neurals, neural VIII was octagonal. However, the neurals posterior to neural IV are typically hexagonal, with the terminal element almost always quadrilateral (n = 17). Intervening neurals may be 6A, 6, or 6P in shape, with a high incidence of staggered sutures giving asymmetrical (5A, 5P, 7A, 7P) configurations. Neural I is apparently always quadrilateral.

The neurals of *Chelydra* are characterized by their considerable breadth, forming an unbroken series from the nuchal to the anterior suprapygal, and by their complex, irregular lateral sutures.

Specimens examined: *C. s. serpentina*: PCHP 276, 1152, 2361, 2362; *C. s. acutirostris*: PCHP 282; *C. s. osceola*: PCHP 273, 275, 489, 797, 1123, 1163, 1629, 1770, 2122, 2308, 2360, 2363; *C. s. rossignonni*: PCHP 274.

Macroclemys

In *Macroclemys temminckii*, the neurals are broad and form an unbroken series from the nuchal to the suprapygal. In the modal condition, the neural configuration is 4–6A–8–6P–6P–6P–6P–4–6 (or 6A). A single octagonal neural

is usually present (12 out of 16 specimens), most commonly at position III (n = 8), but sometimes position II (n = 3) or position VI (n = 1). In some individuals unilateral or bilateral displacement of sutures may alter neural I to a 5P (n = 2) or 6P (n = 2) condition. In others the octagonal neural may be reduced to a heptagonal (rarely hexagonal) condition by suture displacement. Usually eight neurals are present (n = 13), but there may be seven (n = 2) or nine (n = 1). A feature not shown in the illustration provided by BOULENGER (1889: 25) but nearly always present is a very short, tetragonal seventh neural (n = 14), making contact laterally only with pleurals VII. In one specimen, this short neural was further reduced along the midline so that it was divided into two symmetrical elements by a median contact between neurals VI and VIII. The short neural VII is preceded by several (most frequently three) 6P neurals, and followed by a 6 or 6A element. Occasionally (n = 1), neurals I to VI may all be hexagonal-P in shape.

Specimens examined: PCHP 337, 958, 959, 1032, 1256, 1561, 2344—2353.

Kinosternidae

Claudius

COPE (1865) described *Claudius angustatus* as having eight neurals, with only the last pair of pleurals (= costals) meeting on the midline. However, this is not the typical condition; indeed, the neural bones of *Claudius* are extremely unstable. In a series of twelve specimens, neural I is consistently tetragonal and narrow (especially anteriorly). The remaining neurals are much broader. Neural II may be octagonal (n = 5), hexagonal-A (n = 3), or heptagonal-A (n = 4). When neural II is octagonal, neural III is tetragonal, and virtually square (n = 4) or hexagonal-P (n = 1). A heptagonal neural II is followed by a similarly asymmetrical (heptagonal-P or pentagonal-A) neural III. The remainder of the series is usually composed of hexagonal-A neurals, at least in positions IV and V. The neurals may number seven (n = 6), six (n = 5), or eight (n = 1). In specimens with eight pairs of pleurals, pleurals VII always meet medially and pleurals VIII usually do but may be separated by the suprapygal or by a posterior process of one of the seventh pleurals (n = 2). In the specimen with nine pairs of pleurals, pleurals VIII made median contact but pleurals IX were separated by the suprapygal.

Specimens examined: PCHP 480, 482, 483, 516—521, 803, 805, unnumbered.

Kinosternon

The paucity of published information on neural configurations in this widespread, abundant, and extensively studied genus is astonishing. Among the few references in the literature to neural configurations in *Kinosternon* are the following:

15*

PRITCHARD (1969a) illustrated a bony shell of *K. herrerai*, the caption drawing attention to the presence of only four neural bones.

IVERSON (1981) observed that the first neural bone was in contact with the nuchal bone in 41% of *K. sonoriense* and in 10% of *K. hirtipes* but never in *K. integrum*.

BERRY and LEGLER (1980) reported that a male specimen of *K. alamosae* had six neural bones, and a female had five, the seventh and eighth and part of the sixth pair of pleurals being separated by the neural series, and the nuchal bone and the first neural being separated. All hexagonal neurals were long--sided and tapered anteriorly (i. e. 6P in shape).

LEGLER (1965) reported that *K. angustipons* was characterized by five juxtaposed neural bones, the first separated from the nuchal; neurals were hexagonal-P in shape; and pleural pairs I, VI, VII, and VIII were in median contact (the last narrowly so). A small, subtriangular anterior suprapygal was present in two of three specimens. *K. leucostomum* differed from *K. angustipons* in having three or four pairs of pleurals in broad median contact, and in the absence of the anterior suprapygal.

In general, the neural series in *Kinosternon* shows a strong tendency towards elimination of elements towards the posterior of the series, and a significant but lesser tendency towards reduction or sometimes elimination of neural I. Most neurals are 6P in shape, although first and last elements may be otherwise; also, the penultimate neural is often quadrilateral.

Configurations observed in some individual species of *Kinosternon* are as follows:

Neural reduction was least developed in a specimen of *K. flavescens*, in which the neurals had configuration 5–7A–6P–6P–4–6A–7, and only pleurals VIII had a median line of contact.

In five specimens of *K. subrubrum* (subspecies *subrubrum* and *steindachneri*), one had six neurals and the remainder seven. The first three were always 6P in shape, but there was high variation posteriorly; observed configurations from neural IV onwards were: 6P–5P–5A–5; 4–6A–7; 6P–4–7; 6P–4–8–3; and 4–6A–6A–5. In all specimens neural I made contact with the nuchal, but pleurals VII and VIII made median contact (one specimen had a ninth pair of pleurals, also with median contact). A specimen of *K. s. hippocrepis* differed from the other subspecies in having pleural pairs I, VI, VII, and VIII in median contact.

A slightly more advanced degree of neural reduction was evident in 15 specimens of *K. bauri*. Six neurals were present in eleven specimens, and five in four specimens. The anterior element was pentagonal (n = 10), triangular (n = 2), hexagonal (n = 1), heptagonal (n = 1), or octagonal (n = 1). Usually the series terminated in the combination 4—5, although in two specimens the tetragonal neural was displaced forward by one place, and in one case by two places. Pleural pairs I, VI, VII, and VIII made median contact in six specimens; VI, VII, and VIII in five specimens; VI and VII in one; VII and

VIII in one; I, V, VI, and VII in one; and I, V, VI, VII, and VIII in one. In cases where pleurals VIII were separated, the suprapygal intervened.

In ten specimens of *K. herrerai*, neurals ranged in number from four (n = 2), five (n = 3) to six (n = 5). In all specimens, pleural pairs I, VI, VII, and VIII made median contact; in addition, narrow contact between left pleural V and right pleural VI was evident in one specimen, and in another very narrow median contact existed between pleural pairs II and V. Neural II was octagonal in three specimens, and heptagonal-P in a fourth; the series terminated in a triangular element (n = 1), a tetragonal element (n = 3), or in a pentagonal element (n = 6). A ninth pair of pleurals, separated by a suprapygal, was present in two specimens.

Among six specimens of *K. hirtipes*, one had four neurals, one five, and four had six. All had pleural pairs VI, VII, and VIII in median contact, and in five cases pleurals I made contact also. Neural I was triangular (n = 4), tetragonal, or heptagonal, and the posterior neural was pentagonal (n = 3), triangular (n = 2), or tetragonal. In five of the six cases, neural II was octagonal, and in one case neural V was also.

In a series of 17 *K. scorpioides*, neurals numbered four (n = 2), five (n = nine), or six (n = 5). In almost cases, pleural pairs I, VI, VII, and VIII had midline contact, but in one specimen pleurals VIII were separated by the suprapygal, in another neural I failed to reach the nuchal bone, and in a third the middle neural of five was simply missing, so that right pleural III extended well left of the midline to make broad contact with left pleural III, and narrow contact with left pleural IV. Neural I was triangular (n = 2), tetragonal (n = 2), pentagonal (n = 10), hexagonal (n = 1), or heptagonal (n = 1). The posterior element was triangular (n = 5) or pentagonal. A single octagonal neural (at position II) was present in only two specimens.

In two specimens of *K. integrum*, configurations of 7–6P–6P–6P–3 and 3–8–6P–6P–6P–3 were recorded; pleural pairs I, VI, VII, and VIII had median contact in both specimens.

In eight specimens of *K. leucostomum*, neurals numbered five (n = 5), six (n = 2), or seven (n = 1); in the last, three of the neurals were extremely small. Neural I was always pentagonal, and no octagonal neurals were found. Pleural pairs I, VI, VII, and VIII always made median contact. In addition, the neural series was interrupted between IV and V in one specimen, so that pleurals V also made median contact.

In two specimens of *K. sonoriense*, configurations of 5–6P–6P–6P–6P–3 and 5–6P–5P–7P–5 were found; in both, only pleural pairs VI, VII, and VIII made median contact.

Specimens examined: *K. bauri*: PCHP 184, 186—189, 382, 383, 1198, 1243, 1313, 1319, 1320, 1596, 1694, 1997; *K. flavescens*: PCHP 69; *K. herrerai*: PCHP 197, 199, 203—206, 508, 1096, 1097, 1456; *K. hirtipes*: PCHP 209—212, 1098, 1459; *K. integrum*: PCHP 217, 218; *K. leucostomum*: PCHP 213—21'9 351, 881, 1140, 1403; *K. s. scorpioides*: PCHP 220, 222, 431, 1100, 1637; *K. s. cru-*

entatum: PCHP 221, 223, 340, 1101, 1102, 1491; *K. s. albogulare*: PCHP 341, 1173, 1175, 1177, 1316, 2055; *K. sonoriense*: PCHP 33, 34; *K. s. subrubrum*: PCHP 190, 1175; *K. s. hippocrepis*: PCHP 194; *K. s. steindachneri*: PCHP 191—193.

Staurotypus

The neurals of *Staurotypus salvini* were illustrated by BOULENGER (1889: 31), but the configuration shown is not typical of the genus. In a series of twelve (one *S. salvini*, eleven *S. triporcatus*), the neurals were relatively narrow, and with a typical formula of 4–8–4–6A–6A–8. The series is continuous, making contact posteriorly with an elongate anterior suprapygal. In two specimens the separation of neurals I and II was shifted posteriorly to give a 6P–6P configuration instead of one of 4–8, and in two specimens asymmetrical sutural shifts gave configurations of 4–7A–5A–6A–6A–8 and 4–8–4–7A–5A–8 respectively. In only one specimen was there any median line of contact between the pleurals; in this specimen, pleurals VII had a narrow line of contact.

Specimens examined: *S. salvini*: PCHP 168; *S. triporcatus*: PCHP 161, 163, 165, 166, 168, 1105, 1321, 1449, 1488, two unnumbered.

Sternotherus

Surprisingly, even those (such as TINKLE and WEBB, 1955, or TINKLE, 1958) who have undertaken detailed morphological analyses of the turtles of this abundant genus have made little or no mention of the neural bone configurations. Disgracefully (since two species live in abundance within a mile of where I live), I have not analyzed significant samples myself. Anyway, the neural bones of *Sternotherus* appear to differ little from those of the closely related *Kinosternon*. Six neurals are normally present, primarily 6P in form, with an anterior element of variable shape, typically a tetragonal neural V, and a usually pentagonal posterior element. Pleural pairs VI, VII, and VIII meet medially, and pleurals I usually do (5 out of 6). Octagonal neurals were found in *S. minor* — at positions II and IV in one specimen, at position V in another.

Specimens examined: *S. carinatus*: PCHP 503, 1326; *S. minor*: PCHP 225, 2062; *S. odoratus*: PCHP 224, 1314.

Trionychidae

Chitra

In *Chitra indica*, eight discrete neural bones are present, forming a continuous, posteriorly diminishing series. The eighth pleurals are well-developed and meet on the midline. Only one neural separates pleurals I (i. e. neurals I and II completely fused; MEYLAN, 1984, in counting nine neurals in this species

counted these fused neurals separately). The neurals are relatively wide and quite markedly hexagonal-P in form, at least anteriorly. A point of inflection is reached around neurals V and VI (VI and VII in MEYLAN's terminology), behind which neural VII is hexagonal-A and neural VIII pentagonal. In the single specimen examined, the configuration was 6P–6P–6P–6P–5P–5A–6A–5.

Specimen examined: PCHP 1474.

Cyclanorbis

The neural configurations differ markedly between the two species of this genus. In *C. elegans*, eight or nine neurals are present, the first eight at least forming a continuous series. Neural I (the "preneural" of many authors) is distinct and anteriorly broadened. According to MEYLAN (1984) the eight pleurals, or the seventh and eight pleurals (presumably in cases where there is a separation between the last two neurals) may meet medially. Neurals II to VII are 6P in shape.

Midline carapacial bones differ considerably in the congener *C. senegalensis*. In this species, an isolated prenuchal is present, at least in adults (LOVERIDGE and WILLIAMS, 1957), and although neural I is well-defined and anteriorly considerably broadened, the remaining neurals are highly reduced, irregular in shape, and variable in number. VILLIERS (1955) illustrated a specimen with eight neurals, in which neurals V and VI were both isolated from other neurals by contiguous pairs of pleurals. In two specimens examined, six neurals were present in one (but with only neurals II and III making contact, and all pleural pairs except II making midline contact); and the other had seven, but with only neurals I and II making contact, and all pleural pairs except the first making midline contact. In this species, there is a general tendency for the neurals to get smaller posteriorly.

Specimens examined: PCHP 2358, 2359.

Cycloderma

LOVERIDGE and WILLIAMS (1957) described the neural bones of *Cycloderma aubryi* as including a "preneural" (i. e. neural I not fused to neural II), and totalling eight or nine in a continuous series, with only the posteriormost (eighth) pair of pleurals meeting medially. In *C. frenatum*, these authors reported the same typical configuration, but in one specimen neurals I and II were fused, giving a total of only seven neurals. The neurals "usually" formed a continuous series, and either pleurals VII and VIII, or just pleurals VIII, had median contact.

MEYLAN (1986) reported that the point of inflection between 6P neurals and those of a different form typically occurred at position VIII in both species of *Cycloderma*, and illustrated a specimen of *C. frenatum* in which this was the case.

In the single specimen examined, the neural configuration was 4–6P–6P––6P–6P–6P–4–5, pleural pair VII having a short median line of contact, and pleurals VIII a lengthy line of contact. Neural I was almost circular in shape. Specimen examined: PCHP 2374.

Lissemys

In *Lissemys*, a prenuchal is present (as in *Cyclanorbis senegalensis*) that only makes sutural contact with the nuchal in adults. The "preneural" (or neural I) is not fused to neural II. DERANIYAGALA (1939) reported six to eight neurals in *Lissemys punctata*. Neural I is variable in shape — it may be hexagonal or tetragonal, in the latter case approximately square, or with convex sides, or anteriorly broadened. Apart from the first and last elements, the neurals are generally 6P in shape, but neural II may be equilaterally hexagonal, and the last neural in very variable, ranging from small, oval, and isolated from other neurals to relatively elongate, making contact with as many as three pairs of costals. The point of inflection, from 6P to neurals of other form, typically occurs at position VII (MEYLAN, 1984).

Pleurals VIII, VII and VIII, or VI, VII, and VIII may meet on the midline. Specimens examined: PCHP 1437, 2628.

Pelochelys

SMITH (1931) reported that *Pelochelys bibroni* has seven or eight neurals, forming a continuous series. BOURRET (1941) illustrated a specimen with configuration 6P–6P–6P–6P–6–6–5. MEYLAN (1984) reported the modal neural number as nine (bur counting the fused first two neurals separately — eight discrete elements), with only the eighth pleurals meeting on the midline, and with the point of inflection from 6P to 6A neurals occurring at position VI or VII (V or VI in our terminology). This was borne out by the two specimens examined, in both of which only pleurals VIII made median contact, and in which configurations of 6P–6P–6P–6P–6P–4–6A–5 and 6P–6P–6P–6P––4–6A–6A–5 were found.

Specimens examined: PCHP 2375, 2376.

Trionyx

The neural bones of *Trionyx* are of unusual interest, and their configurations in the Recent species have been analyzed by MEYLAN (1984). This genus (and indeed nearly all members of the family) are characterized by loss of all the peripheral and suprapygal bones. The neural series is continuous (with some rare exceptions illustrated by WEBB, 1962: 471), rather narrow, and nearly parallel-sided, and always makes anterior contact with the nuchal bone (except

in juveniles, when a fontanelle separates the nuchal from neural I), but is generally closed off posteriorly by midline contact between the last pair or pairs of pleurals. In the American species, and occasionally in *T. triunguis*, pleurals VIII may be reduced, rudimentary, or absent (nearly always absent in *T. muticus* and *T. spiniferus*).

In four species (*Trionyx leithi*, *T. hurum*, *T. nigricans*, and some *T. gangeticus*), the first pleurals are separated by two bones. The anterior of these has been called a "preneural" by many authors, but MEYLAN has pointed out that it is simply a foreshortened neural I. In the remaining species of *Trionyx*, only one neural separates pleurals I, and this apparently represents a fused composite of the equivalents of neurals I and II of other turtles. This assumption is supported by the discovery that the two bones may be distinct in hatchling *T. ferox* (CARPENTER, 1981), but fused in adults.

The neurals of *Trionyx* number nine, or eight or nine, in most species, but the modal number is eight in the species from outside southeast Asia (i. e. in North America, Africa, and the Middle East) — seven counting the fused first two as one. The anterior neurals are generally 6P in form, reversing to 6A somewhere in the series via an intervening tetragonal element (or pair of elements separated by an oblique suture). However, oblique sutures, giving pentagonal or heptagonal elements, may occur anywhere in the series. MEYLAN (1984) reports that the neurals typically reverse direction at neural VII in *T. cartilagineus*, *T. formosus*, and *T. subplanus*, at neural V, VI, or VII in the American species and in *T. sinensis*, and at neural VI or VII in the remaining species. He reported that the neural series separates all of the pleurals only in *T. subplanus* (as illustrated by BOURRET, 1941: 201), but WEBB (1962) found separation of all pleurals by neurals in 14 of 34 *T. muticus* examined, and in one of 60 *T. spiniferus*. When the posterior neurals meet behind the neural series, the posterior neural is generally pentagonal.

ATATÜR (1979) illustrated a "normal" carapace of *T. triunguis*, with seven neural bones and with a point of inflection from 6P to 6A at the tetragonal neural V. The small neural VII was absent in two illustrated variants, and in two cases pleurals VIII were absent, as is typical of *T. spiniferus* and *T. muticus*. On the other hand, LOVERIDGE and WILLIAMS (1957) reported eight neurals, without qualification, in this species, as well as eight pairs of pleurals, the eighth (and sometimes the seventh) in contact medially. Possibly there are regional differences between the African specimens examined by LOVERIDGE and WILLIAMS and the Turkish ones studied by ATATÜR. It should also be borne in mind that the two different means of counting the neurals of *Trionyx* (i. e. counting the fused neurals I and II as one or as two elements) may lead to ambiguity. However, I believe that MEYLAN (1984) is the only major authority to count these fused bones as two.

In a series of nine *Trionyx ferox*, a bewildering variability was apparent. Seven had seven neurals, and two had six (cf. WEBB, 1962, who found 14 with seven and two with eight in a series of 16). Neurals I and II were usually 6P

except in two cases (4 and 5P respecively). In only four specimens was the reversal from 6P to 6A achieved by a single tetragonal bone (at position III, IV, IV, and V respectively); in others it occurred at a pair of neurals with an oblique interneural suture (at III/IV; IV/V; II/III), and in one specimen the configuration was truly unusual (4–7P–5P–7P–6–6–5, each of the hexagonal neurals being asymmetrical, making unilateral anterior and posterior contact with pleurals on opposite sides of the shell). In this specimen, an eighth pleural was present on the left only.

WEBB (1962) reported seven neurals in 52 of a series of 60 *T. spiniferus*, and eight in the remaining eight. In addition, WEBB reported the presence of only six neurals in USNM 95193. PCHP 1480 (*T. s. hartwegi*) has only six neurals.

MEYLAN (1984) reported that octagonal neurals may occur in *T. sinensis*, with the point of reversal of neurals occurring no further back than position V, but BOURRET (1941: 208) illustrated one with configuration 5P–7P–6P–6P––6P–4–6A–5 (i. e. reversal at neural VII in MEYLAN's terminology). BOURRET also illustrated a *T. steindachneri* with configuration 6P–6P–6P–6P–6P–4–5.

Specimens examined: *Trionyx ferox*: PCHP 354, 1171, 1532—1534, 2051, 2333, two unnumbered; *T. spiniferus emoryi*: PCHP 1437; *T. s. hartwegi*: PCHP 1480; *T. m. muticus*: PCHP 1611, unnumbered; *T. subplanus*: PCHP 1791; *T. cartilagineus*: PCHP 484, 1310; *T. sinensis*: PCHP 3213; *T. triunguis*: PCHP unnumbered; *T. hurum*: PCHP 2629, 2630.

Dermatemyidae

Dermatemys

The shell of *Dermatemys mawi* illustrated by BOULENGER (1889: 28) is atypical of the species in having only seven pairs of pleurals. In this species, the neurals are very narrow, and six or seven in number. Neural I is usually tetragonal and the remainder hexagonal-A except for the usually pentagonal terminal element. Pleurals VII and VIII, or VI, VII, and VIII meet on the midline. Posterior to the continuous series of usually six neurals, an additional median bone is present; most commonly, this makes contact posteriorly with the large suprapygal and in such a case may be considered as a second, small suprapygal. However, this element may be isolated from both the large suprapygal and the posteriormost of the six or seven contiguous neurals. In such cases the bone should be considered part of the neural series.

Specimens examined: PCHP 16—19, 70, 227, 914, 1525.

Platysternidae

Platysternon

In *Platysternon megacephalum*, the neurals are fairly large and broad, and the original configuration of the series was probably 4–6A–6A–6A–6A–6A–6–6. However, there is a marked tendency for the neurals to shift sutures unilaterally or bilaterally, and at least in the anterior part of the series for the transverse sutures separating neural elements to coincide, rather than alternate, with the interpleural sutures. In the two specimens examined, configurations of 4–6A–7A–5A–6A–6A–6–6 and 4–7P–5P–5A–6A–6A–6–6 were found. However, BOULENGER (1889: 47) illustrated a specimen with only seven neurals (6P–5P–4–6A–6A–6). BOURRET (1941) illustrated one with configuration 4–6P–4–6P–4–6–6–6.

Specimens examined: PCHP 1985, 2015.

Carettochelyidae

Carettochelys

In *Carettochelys insculpta*, the neurals are very narrow, somewhat rudimentary, and subject to erratic interruption by contiguous pleurals throughout the series. In one specimen examined, all pleural pairs except III met on the midline, while of the seven neurals present, only II to V formed a continuous series. All neurals were symmetrical, kite-shaped, 6A, or symmetrically pentagonal (i. e. kite-shaped but with a truncated apex) in shape.

In another specimen, homologs of neurals I—IV, forming a continuous series, were present, but neurals I to III were transversely divided into approximately equal halves; in such cases, two neurals together gave a 6A configuration. The homologs of neurals V and VI (actually neurals VIII and IX in view of the divisions in the anterior part of the series) were isolated and kite-shaped, so that pleural pairs IV to VIII all had at least a short median contact.

The neurals of *Carettochelys* are probably very variable. HUMMEL (1929) illustrated a specimen with seven neurals, of which I to VI formed a continuous series, and only pleurals V to VIII had median contact. BOULENGER (1889) characterized the genus *Carettochelys* as having six neurals, all separated from one another by the pleurals, all pairs of which met on the midline.

In post-hatchling specimens, the neurals lie flush with the overall shell surface, but in hatchlings they protrude as a series of leaflike structures along the median keel.

Specimen examined; PCHP 14; BM(NH) 1903.7.10.1.

Dermochelyidae

Dermochelys

Neural bones are lacking in *Dermochelys*, as are the pleurals, peripherals, suprapygals, and pygal. Only a (well-developed) nuchal bone is present.

Cheloniidae

Caretta

In *Caretta*, the anterior neurals are generally somewhat elongate and 6A in shape, but towards the posterior part of the series posterior reduction of individual elements frequently occurs, resulting in isolated neural elements and contiguous posterior pleural pairs. DERANIYAGALA (1939) examined neurals in a series of twelve *Caretta caretta* from Sri Lanka. In three cases, eleven neurals were present in a continuous series, with no midline contact between any pleural bones. In one case there were ten neurals, but the posterior elements were small so that neurals VIII, IX, and X were isolated and pleural pairs V, VI, VII, and VIII made midline contact. Nine neurals were present in four cases. In one, neurals VIII and IX were isolated, and pleural pairs VII and VIII made midline contact. In a second, neural IX and pleural pair VIII made median contact. In a third, neurals VI and VII were isolated, and neurals VIII and IX made contact only with each other; pleural pairs V, VI, and VII made median contact. In the fourth, neurals V, VI, and VII formed an isolated "island", and neurals VIII and IX were individually isolated, and pleural pairs III, VI, VII, and VIII made median contact. In two specimens, eight neurals were present, VIII, and VII and VIII, respectively, being isolated, and pleural pairs VII and VIII making median contact. In two cases, seven neurals were present, in one the neurals forming a continuous series with pleural pairs VII and VIII making contact behind, and in the other neurals V, VI, and VII were isolated, with pleural pairs IV to VIII making median contact.

In a series of seven Atlantic specimens, somewhat comparable variation was found, with the following configurations:

4–6A–6A–6A–6A–5–3 (pleural pairs VII and VIII making median contact between neurals VII and VIII).

4–6A–6A–6A–6A–5–4–(fragment)–(fragment). (An additional azgous bone partially separated neurals I and II, and pleural pairs VI, VII, and VIII made median contact between the last four neurals).

4–6–6A–6A–6A–6A–6A (neural II unusually short).

4–6A–6A–6A–6A–6A–5 (pleural pairs VII and VIII in median contact).

4–6–6P–4–6A–6A–6A–5–4–(fragment). (Pleural pair VI separates neurals VIII and IX, and pleurals VIII separate neurals IX and X).

4–6A–6A–6A–6A–5–(irregular shape). (Pleural pairs VII and VIII separate last two neurals).

4–6–6A–6A–6A–6A–6A–6A–6–4 (neural II very short; no median pleural contact). Specimens examined: PCHP 491, 1030, 1031, 2426, 2427, 2428.

Chelonia

In *Chelonia mydas* (and presumably in *C. agassizi* also), the neural bones form a continuous series from the nuchal bone to the first suprapygal. The individual elements are generally 6A in shape (except for the tetragonal neural I), the anterior ones being distinctly narrow and elongate but with progressive shortening towards the rear of the series. Most commonly they number ten, sometimes nine or eleven. However, difficulty may be encountered in establishing a definite distinction between neurals and suprapygals at the rear of the series; in the specimen examined, there was a thin ridge along the midline of the visceral surface of elements VIII and IX, which may have developed with ontogeny into a sutural connection with the underlying dorsal vertebrae (thus converting a "suprapygal" into a "neural", as the terms are generally defined).

Deviations from the condition described above are quite common, and although the "primitive" neural count is nine (including the small element bridging the posterior part of the separation between pleurals VIII), DERANIYAGALA (1939) found that most Sri Lanka specimens had ten neurals. The additional element usually occurs at the front of the series, so that the first costals each make contact with three neurals. DERANIYAGALA found this in seven of eleven specimens examined. In such specimens, neurals I and II are foreshortened.

Specimen examined: *C. mydas*: PCHP 1735.

Eretmochelys

DERANIYAGALA (1939) found nine to eleven neurals in a series of six *Eretmochelys imbricata* from Sri Lanka, although as with *Chelonia* the distinction between the last neural and the first suprapygal was somewhat judgemental. In such cases, it may be better to define a suprapygal as a bone significantly broader than the preceding neural bones rather than as a midline bone without sutural attachment to a dorsal vertebra.

For the most part, the neural bones of *Eretmochelys* are similar to those of *Chelonia*, i. e. generally 6A in shape, and relatively long and narrow, decreasing in size posteriorly. However, it is quite frequent for the first two neurals to be foreshortened so that the first costals make contact medially with three neurals. DERANIYAGALA found this in five of six specimens examined. Normally there is no median connection between any of the pleural bones in *Eretmochelys*.

In three specimens examined, the following neural configurations were

encountered: 4–6A–6A–6A–6A–6A–6A–6; 4–6A–6A–6A–6A–6A–6A–6P–4; 4–6P––4–6A–6A–6A–6A–6A–6–4.

Specimens examined: PCHP 2054, 2429, 2430.

Lepidochelys

In *Lepidochelys*, extensive transverse, and occasionally longitudinal, division of neural bones occurs, resulting in higher neural counts (up to fifteen) than in any other Recent turtle genus. The neural series is comparatively narrow, and (except in rare cases) forms an unbroken series from the nuchal bone to the anterior suprapygal. In most specimens the neural series may be perceived as one in which the primitive configuration of elongate, 6A neurals is modified by transverse division of each such neural into a short hexagonal anterior element and a small, tetragonal posterior one. DERANIYAGALA (1939) illustrates and describes the neural configuration in several specimens of *L. olivacea*; in most specimens, the majority of the pleural bones each make contact with three neurals; only pleural pairs I, VII, and VIII are customarily separated by only two neurals. PRITCHARD (1969 b) illustrates neural configurations for three *L. olivacea* from Pacific Mexico; in one, the homologs of neurals III, IV, and V are transversely divided; in the second, the homologs of neurals III, IV, V, VI, and VIII are transversely divided; and in the third, the homologs of neurals II, III, IV, and VI are transversely divided.

The situation is similar in the congener *L. kempi*. Four bony carapaces examined had configurations 4–6A–6P–4–4–6P–4–6–4–6P–4–6–6P; 4–6A–4–6–4––6P–4–6–4–6A–6–6P–4; 4–6A–6–4–6–4–6–4–6A–6–4–6–4 (with three azygous intercalations, not counted); and 4–6A–4–6–4–6–4–4–6A–4–6A–6–6P–4.

In three others illustrated by PRITCHARD (1969 b), the configurations were: 4–6–4–4–6A–6–4–6A–4–6A–6P–4–5–3, with short median contact between pleurals VIII between the last two neurals; 6P–4–6A–6A–6A–6A–6–4–6–4; and 4–6–4–6–5P–3–5A–6A–6A–6A–6–4, with contact on the left side between neurals V and VII.

Specimens examined: *L. olivacea*: PCHP 1110—1112; *L. kempi* PCHP 1113, 1115, 1116, 1224—1226, 1978.

Natator

This genus was informally revived, for *Chelonia depressa*, by PRITCHARD and TREBBAU (1984), and a detailed account justifying this change is currently being prepared by ZANGERL et al. (in press). The neurals of *Natator* are basically of the elongate 6A form, but are subject to some individual variation — primarily transverse division—near the ends of the series. PCHP 2394, with a configuration of 4–4–6–6A–6A–6A–6A–6A–6A–6A, may be considered reasonably typical; in four other specimens, pleurals II made contact with three

neurals, and in one of them pleurals I and VI did also. The total neural count ranged from ten to twelve.

Specimens examined: PCHP 2394; BPBM 8292, 8294, 8295, 8299.

Cheliidae

Acanthochelys

This genus was recently revived to accomodate all of the species of *Platemys* except *P. platycephala*, i. e. *Acanthochelys pallidipectoris*, *A. spixi*, *A. radiolata*, and *A. macrocephala* (McBee et al., 1985). As far as is known, neural bones are uniformly lacking in this genus.

Chelodina

Although *Chelodina* has often been described as lacking neurals (e. g. by Williams, 1953), in fact they are consistently present in the southwestern species *C. oblonga* (Burbidge et al., 1974). These authors found that, in nine specimens from near Perth, one had five neurals, three had six, four had seven, and two had eight. A figured specimen with eight neurals showed a narrow species of contiguous (except for neural VIII) elements of irregular but generally vaguely 6A shape. Neural I was small and separated from the nuchal bone, and neural VIII isolated and rudimentary. Burbidge et al. reported that in those specimens with fewer than eight neurals, one or more of the most anterior or the two most posterior were missing.

In six specimens examined, the following configurations were found: i) Neurals seven, I rudimentary, VI and VII isolated; pleural pairs I, VI, VII, and VIII in median contact. ii) Neurals six, all contiguous; pleurals I, VI, VII, VIII in median contact. iii) Neurals eight, I rudimentary, VIII isolated; pleurals I, VII, and VIII in median contact. iv) Neurals five, V isolated; pleurals I, V, VI, VII, VIII in median contact. v) Neurals six, all contiguous; pleurals I, VI, VII, VIII in median contact. vi) Neurals seven, VII isolated, pleurals I, VI, VII, VIII in median contact.

Rhodin and Mittermeier (1977) also found neural bones in *C. oblonga* (five and eight respectively in the two specimens examined), and additionally reported on the occurrence of neurals as a minority or casual condition in other species of *Chelodina* — one was found in one of 12 *C. longicollis*; two in one of eight *C. siebenrocki*; and neurals (one, two, two, three, and four respectively) were present in five of twenty specimens of *C. novaeguineae* examined. None were present in four *C. steindachneri*, two *C. expansa*, four *C. rugosa*, or three *C. parkeri* examined by Rhodin and Mittermeier. I also found none in three *C. expansa*, but in one of five *C. rugosa*, four isolated neurals of posteriorly diminishing size were present, behind pleural pairs II, III, IV, and V respectively; all pleural pairs made midline contact.

The illustrations of the carapace of *C. oblonga* shown by BOULENGER (1889: 214) and discussed by ZANGERL (1948) were probably based upon a misidentified *C. rugosa* (RHODIN and MITTERMEIER, 1977), or upon a specimen of an undescribed *Chelodina* species from the Kimberleys (nothern Western Australia).

Specimens examined: *C. oblonga*: PCHP 2415—2419, 2422; *C. rugosa*: PCHP 2409—2413; *C. expansa*: PCHP 2396—2398.

Chelus

Chelus fimbriatus is unusual among chelids in having well-developed neurals; they are, in fact, both broad and thick. They vary in number. WOOD (1976) found seven neurals in each of fifteen specimens, and eight in each of four others. In a series of 22 specimens (four of which were also examined by WOOD), I found seven neurals in 16, six in 2, and eight in 4. In the typical configuration, neural I is elongate, corresponding to the enlargement of the first pleurals, but usually tetragonal, although in a few cases it makes narrow contact with pleurals II. Posteriorly, the neurals are mostly hexagonal-A in shape, but variable in length. Neural II is short, neural III distinctly longer, neurals IV and V short, and neurals VI and VII usually much longer than IV and V, together forming the upslope of the high tubercle under the fourth vertebral scute, to which the two bones make very variable contributions. Reduction of the neural count to six corresponds to replacement of neurals VI and VII by a single elongate bone, contacting no fewer than four pleurals (V to VIII) on each side. Increase to eight neurals occurs by transverse division of neural I (n = 2), or neural VII (n = 1), or by insertion of an azygous element beside neural I (n = 1).

Nearly always, pleurals VIII meet behind the posteriormost neural, separating the latter from the single triangular suprapygal. WOOD (1976) reported only four of nineteen specimens to have all of the neurals separated medially, and I found this in three out of 22. In the latter three cases the suprapygal extended further forward than usual, forming the downslope of the high tubercle under vertebral scute IV. In the other 19, the eight pleurals were asymmetrically contiguous; sometimes the asymmetry was so marked that the last neural made contact with only one of the eighth pleurals. The high tubercle under vertebral IV was usually approximately symmetrical, although usually some degree of deflection to the left was evident.

Specimens examined: PCHP 37—40, 42, 43, 1037, 1039, 1209, 1210, 1229, 1230, 1335, 1337, 1338, 1823, 1910, 2157, 2158, unnumbered; UF/FSM 21977, 22266.

Elseya

Elseya almost always lacks neural bones. However, RHODIN and MITTERMEIER (1977) found four in one of nine specimens of *E. latisternum* examined, and three in an additional specimen of uncertain species. Nineteen *E. novaeguineae* all lacked neurals.

Specimens examined: *E. latisternum*: PCHP 446; *E. novaeguinae*: PCHP 1057, 1058.

Emydura

Recent *Emydura* apparently consistently lack neural bones; RHODIN and MITTERMEIER (1977) found none in 31 *E. subglobosa*, 8 *E. kreffti*, and 1 *E. macquari* examined. I found none in two specimens of *E. signata*, in one *E. macquari*, in four *E. australis*, or in seven specimens of an undescribed species from Fraser Island, Queensland. However, WARREN (1969) found a neural bone in a fossil (Oligocene or Miocene) specimen attributed to *E. macquari* from Tasmania.

Specimens examined: *E. macquari*: PCHP 1041; *E. australis*: PCHP 2377, 2406—2408; *E. signata*: PCHP 436, 438; *Emydura* (Fraser Island): PCHP 2399—2405.

Hydromedusa

Hydromedusa resembles *Chelus*, but differs from other chelid genera, in having substantially unreduced neurals. The neural series is relatively narrow, usually continuous, and composed primarily of hexagonal-A elements. The following configurations were found in three specimens of *H. tectifera*:

4–6A–6A–6A–6A–7–4 (pleurals VII and VIII meet medially; pleural VII is small and asymmetrically displaced to the left, so that neural VI contacts right pleural VII).

4–4–6A–6A–6A–6A–5 (pleurals VII and VIII meet medially; suture between neurals I and II virtually continuous with sutures between pleurals I and II).

4–6A–6A–6A–6A–6A–5–4 (neural VIII is very small, rhomboidal, and isolated from both the other neurals and from the suprapygal, being inserted into the median suture between pleurals VIII. Pleurals VII and VIII make median contact).

WOOD and MOODY (1976) reported that *H. tectifera* had six neurals, but illustrated a specimen (BMNH 54–5–16–11) with seven. They also reported seven to nine neurals for the rare congener *H. maximiliani*, based upon examination of six bony carapaces. Contact between neural I and the nuchal bone is constant but narrow, and whilst the neural series is continuous it may or may not be separated from the suprapygal by medially contiguous pleurals VIII. The overall neural shape is hexagonal-A (with the terminal element pentagonal), but anteriorly the interneural sutures are almost continuous with the interpleural sutures, so that the anterior neurals are almost rectangular.

Specimens examined: *H. tectifera*: PCHP 1334, 1335, 1625.

Phrynops

Neural variation is greater in the genus *Phrynops* than in any other. Even though data are not available for several of the described species, those that have been investigated show neural configurations ranging from a nearly

complete series to absence of all neurals. Even within a species, variation may be remarkable, as in the cases of *P. nasutus* and *P. gibbus*.

WOOD (ms.) reported that a series of fifteen *P. geoffroanus* showed contiguous series of five to seven neurals, 6A in form except for the terminal elements, and with one to three of the posteriormost pleurals in contact. A generally similar configuration has been reported by RHODIN and MITTERMEIER (1983) for *P. williamsi*; two specimens, typified by BMNH 84.2.5.1, showed identical configurations of 4–6A–6A–6A–6A–5, with pleural pairs VI, VII, and VIII making median contact.

SIEBENROCK (1904) illustrates the neural configuration of a specimen of *Phrynops rufipes*, in which a continuous series of seven neurals is present, N1 in contact with the nuchal bone neurals II to VI 9A in shape, and neural VII elongate and heptagonal, the posterior tip entering the suture between pleurals VIII.

Three specimens of *P. hilarii* were examined. The archetypal configuration appeared to be 4–6A–6A–6A–6A–5, with neural I distinctly elongate compared to the others. In one specimen the first two were shifted to 5P–5A, and in another a small rhomboidal element was intercalated into the suture separating pleurals VI. In all, pleurals VI to VIII made median contact. BOULENGER (1889: 221) illustrated a specimen with configuration 4–6A–6A–6P–6A–5.

Considerable neural reduction was found in *P. nasutus*. While this species may have as many as five neurals (BOUR, 1973), and BOULENGER (1889: 218) illustrated one with four (the fourth isolated), in the three specimens examined two had lost all neurals, and the third had only three (all pleurals except II and III meet medially). Somewhat comparable, but highly variable, reduction was found for *P. gibbus* by PRITCHARD and TREBBAU (1984). Neurals in a series of nine specimens (eight from the MLS collection, Bogotá) ranged from zero to five, the series being composed of 6A, kite-shaped, or rhomboidal elements forming contiguous series or with one or two breaks. Pleural pairs I and V to VIII always made median contact, and neurals II to IV did sometimes also. In three specimens additional to those figured, two had four contiguous neurals (pleural pairs I, V to VIII in median contact); and one had a single fragmentary neural only, partially separating the anterior half of interpleural suture II.

In two specimens of *P. zuliae* examined, neurals were absent, as they were in two specimens of *P. dahli* examined by ZANGERL and MEDEM (1958).

Specimens examined: *P. gibbus*: PCHP 434, 435, 439, 1818; *P. hilarii*: PCHP 1328—1330; *P. nasutus*: PCHP 440, 1060, 1062; *P. zuliae*: PCHP 1700; FSM 53440; *P. vanderhaegei*: MNHNP, two unnumbered.

Platemys

Neural bones were absent in all of the specimens examined, and ERNST (1985) reported that neural bones were "usually absent" in *Platemys platycephala*, the eight pairs of pleural bones meeting on the midline. However,

A. RHODIN (pers. comm.) reports the occasional presence of some rudimentary neurals in this species, and a single such element was present in PCHP 2519.
Specimens examined: PCHP 442—444, 1526, 2519, unnumbered.

Pseudemydura

Neurals are apparently consistently lacking in this rare, monotypic genus (BURBIDGE, 1967; BURBIDGE et al., 1974; RHODIN and MITTERMEIER, 1977).

Rheodytes

LEGLER and CANN (1980) examined three complete and sixteen partial skeletons of *Rheodytes leukops*, and found the neural bones to be consistently lacking. None were present in the single specimen I examined.
Specimen examined: PCHP 2390.

Pelomedusidae

Erymnochelys

BROADLEY (1983) wrote that *Erymnochelys madagascariensis* had six neural bones, in which respect it would thus differ notably from *Podocnemis*, in which seven are almost always present (in Recent forms). TRONC and VUILLEMIN (1974), however, in a detailed description of the osteology of this taxon, noted that seven neurals are present in young specimens, but that the last two are liable to fuse in old animals. Neural I (according to these authors) is rectangular, three times as long as wide; neural II has the shape of an elongated hexagon; neurals III to V are irregularly hexagonal in shape, wider and shorter than neural II and progressively decreasing in size; neural VI is of almost regular rectangular shape, and neural VII is small and pentagonal. Pleural pairs VII and VIII have a median line of contact.

Pelomedusa

BROADLEY (1983) examined the neural configurations of 25 specimens of *P. subrufa*. Seven neurals were present in twenty; three included a reduced (eighth) neural; and in two only six neurals were present. Neurals were generally 6A in shape, and reduction took place from the rear, so that pleurals VIII, or VII and VIII, made median contact. In some specimens the tetragonal neural I was anteriorly narrowed, but it was reduced to the point that it was widely separated from the nuchal only in FMNH 17160.

Peltocephalus

Peltocephalus dumerilianus usually has seven neural bones (six specimens examined), with configuration 4–6A–6A–6A–6A–6A–5. The neurals are relatively broad in external aspect, but are considerably narrower when viewed

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from visceral aspect, as a result of flanges on the proximal ends of the pleurals that partially cover the undersides of the neurals. Typically, pleural pairs VII and VIII make median contact. In one specimen (PCHP 1354), although neurals I to VI had the normal contrast between broad external and narrow visceral aspects, neural VII was clearly visible in visceral aspect but was completely obscured dorsally by the midline suture of pleurals VII.

Specimens examined: PCHP 1351—1356.

Pelusios

Although the variable neural configurations in this complex genus were ignored for a long time, the recent studies of BROADLEY (1981, 1983) have provided much insight.

In *Pelusios*, the neurals usually form a continuous series of primarily hexagonal-A elements of relatively narrow form. However, there is a moderate tendency towards reduction of neural I so that it is separated from the nuchal bone by contiguous pleurals I, and there is a strong but variable tendency towards reduction of the posterior neurals, so that pleurals VIII, at least, meet on the midline.

Configurations found by BROADLEY are as follows:

Pelusios subniger: usually eight neurals are present, continuous but separated from the single suprapygal. In two of twenty specimens neural VIII was lacking, and in three others two suprapygals were present.

P. nanus: three of four specimens lacked neural VIII; in the other, neural VIII met VII at a point only. Neural I is anteriorly narrowed, meeting the nuchal at a point or narrowly separated from it.

P. b. bechuanicus: 13 specimens all had a continuous series of eight neurals, separated from the suprapygal. Neural I failed to contact the nuchal in two cases. In two examples of *P. bechuanicus upembae*, one was similar to the above, and the other had an elongate, transversely divided neural VIII.

P. rhodesianus: eight neurals are always present (n = 28), neural I contacting the nuchal. Neural VIII may be elongate so as to meet the suprapygal. Neural VIII, or VII and VIII, may be isolated.

P. sinuatus: usually six or seven neurals present (neural VIII always absent, neural VII reduced, sometimes absent). Neural I fails to reach the nuchal; in one of 50 specimens it was absent. Specimens from the Lake Tanganyika area may have only five neurals, with neural V reduced or absent, leaving neural VI isolated.

P. castaneus: geographic variation in neural configuration also occurs in this species. In the typical form (n = 8), a continuous series of eight neurals is separated from the suprapygal. In *P. c. williamsi*, the elongate neural VIII

is only narrowly separated from the supracaudal in one specimen, and in another neural I is lacking. In a paratype of *P. c. lutescens*, neural I is lacking and neural VIII reduced and well separated from the suprapygal. In eight specimens of *P. castaneus castanoides*, five to seven neurals are present, well separated from both nuchal and suprapygal. Neurals I, VII, and VIII are reduced or absent. Neurals are reduced or absent at the ends of the series in island populations (Madagascar and Seychelles).

P. gabonensis: in this form, an unbroken series of eight neurals may be present, with neural VIII usually separated from the suprapygal, but in some cases neural VIII contacts the suprapygal, and in some others (three out of five), neural I may be lacking.

P. adansonii: neural I is consistently lacking in seven specimens; neural VIII is lacking in one, but a ninth neural is present in another.

P. niger: in two of three specimens, neural I is reduced or absent, and neural VIII is elongate, contacting the suprapygal.

P. carinatus: the paratype has eight neurals, but neurals VII and VIII are very small and the latter isolated.

BOUR (1986) illustrated the neurals in the holotype of the new species *P. broadleyi*. Neurals I and VIII are absent, so that the neural series, although continuous, is well separated from both the nuchal and suprapygal bones.

I have scant material to amplify BROADLEY's series, but can add that in a specimen of *P. c. williamsi*, eight neurals were present, neural I reduced and well separated from the nuchal, and neural VIII somewhat elongate and relatively narrowly separated from the suprapygal. In two specimens of *P. castaneus* from Guadeloupe, French West Indies, eight neurals were present, the first making good contact with the nuchal, and the eighth either barely entering, or deeply entering, the median suture between pleurals VIII.

Specimens examined: *P. sinuatus*: PCHP 1305; *P. castaneus williamsi*: PCHP 801; *P. castaneus castaneus*: PCHP 475, 1795; *Pelusios subniger*: PCHP 511.

Podocnemis

Although various configurations, including the complete absence of neurals, have been described for fossil *Podocnemis*, among living species the standard neural configuration is 4–6A–6A–6A–6A–6A–5 (WOOD, 1971), with relatively rare deviations. In the typical case, pleural pairs VII and VIII meet on the midline.

BOULENGER (1889: 201) illustrated a minor variation from this configuration — a specimen of *P. sextuberculata* in which the seventh neural is heptagonal and somewhat enlarged, so that it completely separates pleurals VII and partially separates pleurals VIII.

Other variants found include a specimen of *P. vogli* (PCHP 2305) in which neural I extends posteriorly to make narrow contact with pleurals II, neural

II being reduced and tetragonal. This is identical to the configuration described by WOOD (1971) for the Cretaceous species *P. elegans*. Being unaware of the occasional existence of this variant in living *Podocnemis*, WOOD was emphatic that "nothing remotely resembling the shapes of the first two neurals in *P. elegans* is encountered elsewhere in the genus. So conservative in structure is this part of the shell in all other species..."

Actually, I found a couple of other specimens with variant configurations of neural I. In PCHP 1193 (*P. unifilis*), neural I was pentagonal and made unilateral contact with one of the second pleurals; and in PCHP 1509 (*P. expansa*), neural I was reduced so that it was widely separated from the nuchal bone, pleurals I being in midline contact for about half of their width.

In one specimen of *P. unifilis* (PCHP 1051), only six neurals were present, pleurals VI, VII, and VIII having a median line of contact.

In *Podocnemis lewyana*, the neural bones are typical of the genus, but this species is unique in the genus in lacking the suprapygal bone (n = 6; WOOD, 1971).

Specimens examined: *P. expansa*: PCHP 1509, 1510, 2152; *P. unifilis*: PCHP 1044, 1051, 1193, 2165; *P. vogli*: PCHP 1052, 1186, 1366, 1367, 2146—2148, 2305, 2310; *P. erythrocephala*: PCHP 1194.

III. DISCUSSION

The pattern of the bony mosaic of a turtle's shell undoubtedly reflects, to a considerable degree, the phylogenetic history of the Order, and the materials and structures available to the animal with which to assemble the strongest or most appropriate integrated structure. Neomorphic elements occur rarely, and the overall phylogeny of the *Testudines* documents elimination far more frequently than proliferation of individual shell elements. Thus, even though an engineer might be able to design a turtle shell that would be a marked improvement upon the structures actually found, turtles may simply have never undergone the appropriate mutations in their evolutionary history to make such a structure possible.

Some of the variant forms of the neural bone series in living turtles undoubtedly reflect simply the result of a shifting of underlying functional structures or changes in overall shell shape, as is documented below for such conditions as overall widening of the neurals, or posterior shift of the series to a hexagonal-P condition. The resulting structure is not necessarily stronger than the ancestral condition. Some factors too may be under indirect rather than direct genetic control. For example, the octagonal form of certain neurals in testudinids, chelydrids, and other chelonians may reflect genetic programming for something no more complex than enlargement of certain elements. In the hatchling or juvenile, some neurals may simply be larger than others in the series (as illustrated e. g. by PROCTER, 1922). As the animal grows and the shell mosaic

unites, such enlarged neurals may assume an octagonal configuration purely as a result of the way in which the mosaic closes — an enlarged element will make contact not only with the corresponding pleural pair, but also with the pairs immediately anterior and posterior.

Nevertheless, some changes in the neural series appear to reflect actual strengthening of the shell, or resistance to stresses to which certain taxa may be more than usually subject. Thus, while wide-shelled cryptodires, such as *Chelydra*, often have widened neurals, even wide-shelled pleurodires, and especially long-necked wide pleurodires such as *Chelodina steindachneri*, may lack neural bones entirely. This is interpreted below as a response to the asymmetrical stresses imposed upon the neural area of the shell in pleurodires. Moreover, such modifications almost certainly reflect changes that strengthen the overall shell structure without the need to add significantly to shell thickness.

Such arguments assume that a suture represents a weak point in the shell of a turtle. Analysis of the shells of turtles fractured by abrupt trauma, such as by automobile impact on highways, does not necessarily confirm this assumption; the shells of road-killed turtles show little tendency to fracture along suture lines. Nevertheless, I feel justified in proceeding with this assumption for several reasons:

1) In the course of phylogeny, there is a tendency for turtles to reduce the number of both carapacial and plastral bony elements (e. g., the loss of neurals in many chelids; loss of the entoplastron in kinosternines; loss of the mesoplastra in all modern turtles except pelomedusids; loss of peripheral bones in nearly all trionychids). This tendency has rare exceptions (e. g. in *Lepidochelys*), but generally one would assume that selective pressure would tend to eliminate shell bones only if a smaller number of shell bones — and thus fewer sutures — represented an architectural improvement.

2) In nature, predation is most intense upon young turtles, in which the sutures are less tightly knit than in adults, and in which some bones that ultimately unite are still separated by fontanelles. Moreover, the pressures exerted on a turtle shell by a natural predator are likely to be less abrupt than those encountered in a highway impact and while an adult turtle may crack across the bones following the instantaneous impact of an automobile, a young turtle in the jaws of a predator may well be fractured along suture lines. I noticed some tendency towards fracture along sutural lines in the broken shells of specimens of the undescribed, extremely thin-shelled *Emydura* sp. on Fraser Island, Australia, that had been predated by dingoes.

3) For the most part, a turtle shell shows alternation rather than coincidence between seams and sutures. Since a seam, lacking the interdigitations of a suture, is surely a weak point in the superficial keratinous layer of a turtle shell (especially since a seam is reflected in the uderlying bone by a sulcus that may locally reduce the thickness of the bone by a substantial percentage), one would assume that seams would be reinforced by coincident sutures if the latter represented' lines of strength rather than of weakness. In practice, we

find that seams and sutures are only occasionally coincident, as along the midline of the plastron, along the hinge-line of species with kinetic shells, or along the costomarginal seam line of many testudinids and other turtles — especially juveniles. The former line of weakness, however, is strengthened by the entoplastron, while in certain forms with laterally reduced or absent entoplastra, such as cheloniids and kinosternids, some midline kinesis of the midline of the plastron may be possible, and is presumably mechanically desirable in facilitating respiration or shell closure (BRAMBLE et al., 1984). In tortoises, the otherwise vulnerable pleuro-peripheral line is spanned and strengthened by the plastral buttresses and also by the distal tips of the ribs. Furthermore, in some species in which the pleuro-peripheral line is straight and seemingly weak in external aspect, examination of the suture line in visceral aspect shows extensive and complex suturing, as in *Cuora flavomarginata*. Perhaps it is noteworthy too that there is enormous variation in the closeness with which the sutures of a turtle shell interdigitate. For example, the neuro-pleural sutures of *Chelydra* are extremely interpenetrating, while on the other hand the interperipheral sutures of *Caretta* often only show interdigitations close to the external surfaces of the connection, the interior part of the join being a simple abuttment of smooth bony faces.

In *Care tochelys*, the pleuro-peripheral line is not suturally united even in adults. *Carettochelys* has an extensively kinetic shell, with the plastron showing transverse kinesis behind the anterior lobe and longitudinal kinesis along the midline and at the bridges, and possibly some slight kinesis along the pleuro-peripheral line also occurs.

An alternative explanation for the usual non-coincidence of seams and sutures except along lines of kinesis is the possibility that a seam represents a weak point in the shell not just as regards susceptibility to mechanical damage but also to ingress of pathogens. Pathogens may penetrate to the viscera much more readily if the seam is underlain by a suture or a fontanelle rather than by a sheet of continuous bone. It is noteworthy in this respect that in the testudinid *Malacochersus*, in which the bony shell is vastly reduced, the secondary fenestra in the carapace, although extraordinarily extensive, never cross a seam line. Since this species has evolutionarily sacrificed shell rigidity in favor of flexibility, it suggests there may be a physiological rather than, or as well as, mechanical reasons for seams to be underlain by continuous bone.

In addition to the assumption that an unreinforced suture represents a weak point in the turtle shell, it is also assumed that the bones are more important than the scutes in determining the overall strength of the shell. This assumption is certainly correct for many, perhaps most, turtle species, in which the scutes are a small fraction of the thickness of the bones, although even then they may play a valuable structural role in providing "tension members" overlying the more compression-resistant bony layer below. Also, there are some species, such as *Eretmochelys imbricata* and possibly *Geochelone yniphora* or *Manouria emys*, in which the scutes are very thick and the fontanelles in the bony carapace

persistent, in which the scutes probably do contribute significantly to shell strength. In *Eretmochelys*, a form uniquely subject to routine battering by wave action in its coral reef habitat, it is interesting that the scutes are not only uniquely thick, but also the otherwise vulnerable seams are protected by a significant degree of scute imbrication.

Ancestral neural configuration

Variation in neural bone configuration throughout the *Testudines* is most easily interpreted on the assumption that the ancestral condition was one in which the neural bones form a continuous series of relatively narrow hexagons extending from the nuchal bone to the suprapygals, these hexagons being bilaterally but not anteroposteriorly symmetrical. In the primitive condition, a neural bone has its two anterolateral sides shorter than the posterolateral sides, a form perhaps most vividly described as coffin-shaped. This neural configuration is found in turtles of many families, including such diverse forms as the cheloniids, emydids, and some primitive testudinids, as well as in many entirely extinct families. The neurals are also of this form, although may not necessarily form an unbroken series contacting both nuchal bone and the first suprapygal, in pelomedusids, dermatemyids, and others.

The primitive neural configuration serves, in architectural terms, as a keystone to the carapacial arch. Vertical pressure in the neural area serves more to force the neural into closer sutural bonding with the pleural bones rather than to split the arch, as might happen if neurals were absent. The hexagonal rather than rectangular dorsal aspect of the primitive neural simply results from the need to stabilize the shell against extensive transverse cracking that might result if there were an uninterrupted straight suture separating a given neural/pleural unit from its neighbors.

Among living turtles, some of the variations from the primitive neural configuration include the following:

1. Hexagonal neurals with the short sides posteriorly rather than anteriorly.
2. Expansion of odd-numbered neurals so that the series is one of alternating quadrilateral and octagonal elements (at least anteriorly) rather than uniform hexagons.
3. Formation of an octagonal second neural.
4. Loss of all shell sutures by ankylosis.
5. Formation of tetragonal neurals.
6. Posterior interruption of the neural series, with certain of the pleural pairs meeting medially.
7. Loss of both anterior and posterior neurals, in the extreme condition resulting in loss of all the neural bones.
8. Widening of the (hexagonal) neurals.

9. Transverse, and occasionally longitudinal, splitting and consequent proliferation of primitive neural elements.

10. Reduction of some or all neurals to small, isolated, kite-shaped elements.

11. Fusion of neurals I and II, following anterior displacement and compression of the neural series.

Each of these conditions merits further discussion.

1. Hexagonal neurals with the short sides posteriorly

This condition is shown by *Kinosternon* and *Sternotherus* and by several genera of batagurine emydids (*Cuora, Cistoclemmys, Geoemyda, Melanochelys, Heosemys, Rhinoclemmys*, etc.) as well as by certain testudinids, including *Kinixys* and *Homopus*, and occasionally by *Geochelone carbonaria* and *Chersina angulata*. It appears to correspond to a life-style that requires that the head be retracted a considerable distance into the shell. Thus, in the kinosternines, the deep retraction corresponds to modest swimming ability, and with operation of the anterior plastral lobe. The emydids that show this condition are secondarily terrestrial or at most amphibious species. In contrast to their aquatic ancestors that presumably sought safety by rapid retreat (e. g. by diving off logs, or swimming away), for more terrestrial forms defense depends upon stout armor and extensively retractile extremities. Such retractibility engenders a posterior displacement of the dorsal vertebrae, at least in the anterior part of the series. Moreover, since the neural bones typically overlap or alternate with the dorsal vertebrae, for reasons both of embryologic history and of presumed protection of the otherwise vulnerable intercentral areas, posterior displacement of the dorsal vertebrae corresponds to a similar displacement of the neural bones. This causes them to make sutural contact with the pleural bones posterior rather than anterior to those with which the neural has its principal contact. The tortoises that show this condition are those with relatively cylindrical rather than hemispherical shells, and which are able to retract the extremities a considerable distance, presumably a necessity in the face of a particular type of predation pressure.

2. Formation of an octagonal second neural

This condition occurs in two types of situations. It is a frequent feature of turtles that have an unusually large head, such *Macroclemys, Platysternon*, certain *Graptemys* and *Malaclemys, Pseudemys scripta chichiriviche*, and others. In such turtles, it may serve to strengthen the area of the carapace from which the large and heavy head and neck are suspended, by allowing the neural bone on which the strain principally falls to be stabilized by forces transmitted through three pleural bones on each side rather than one or two.

The octagonal second neural condition is also observed in certain members of the *Geoemyda* complex, such as *Rhinoclemmys funerea* and *Melanochelys*

trijuga, even though these species have notably small heads. These species are relatively aquatic members of a complex whose name (*"Geoemyda"* — land turtle) derives from its overall terrestrial preference, and it may be hypothesized that they evolved from more terrestrial species with the typical series of hexagonal neurals with the short sides posteriorly. Re-assumption of an aquatic mode of life may have required that the head and neck be more extensible rather than more retractile, observation of potential danger while basking perhaps being more important than deep retraction. This is facilitated by a secondary anterior displacement of the first dorsal vertebrae, which resulted in an anterior shift in the suture between neurals I and II, causing these to become tetragonal and octagonal respectively, rather than both hexagonal.

3. Alternating neurals octagonal throughout most or all of the series

This condition occurs in the typical, domed, terrestrial species of the family *Testudinidae,* in which the shell sometimes becomes quite thin and the dorsal vertebrae and rib heads greatly reduced, presumably, at least in part, because terrestrial species are constantly subject to gravitational forces and there is selective pressure to reduce shell weight. However, since testudinids (except for oceanic island forms) are still subject to various predators, the bony shell mosaic must be as resistant as possible to fracture under mechanical pressure. Thus, the edges of the shell may be thickened, the shell as a whole assumes a rounded, domelike shape, the plastral buttresses reach high into the carapace, carapacial sutures often become extraordinarily complex and interpenetrating, and the dorsal part of the carapace is often strengthened by the area under each vertebral scute becoming slightly bulbous or domed. Since the jaws of a predator — as well as other burdens such as the weight of the male on the female during copulation — are most likely to impinge upon the apices of these domes, each of them is strengthened by the neural bone under the middle of each vertebral scute assuming an octagonal form, and the pleurals alternate between having their upper and their lower ends expanded. In this way, pressure on the bone under the apex of a vertebral scute is trasmitted through three pleural bones on each side and ultimately to approximately one-third of the linear extent of the pleuroperipheral suture line on each side of the shell.

This suture line itself, which is coincident with the costomarginal sulcus in many tortoises, might appear to be a line of weakness. However, in domed testudinids, this area is essentially vertical, so that pressure applied to the carapace is transmitted as a purely compressive force rather than as a shearing force on the pleuroperipheral suture. The carapace thus forms an "inverted bowl" resting on the "ring" of peripherals, to which it is attached by anterior and posterior sutures and at ten points on each side corresponding to the eight rib tips and two plastral buttresses. Such a structure, while strong, may have just enough "give" at the sides to avoid fracture following stresses that otherwise might have cracked it.

The octagonal neural IV in the high-shelled *Kachuga* species (e. g. *K. tecta*) may have a function similar to that of the octagonal neurals in testudinids; vertical pressure on the carapace of such a turtle would impinge upon the tubercle at the highest point of the shell, which is underlain by neural IV. The pressure would thus be resisted by transmission to three pleural bones on each side of the shell, rather than to just two.

4. Loss of all shell sutures by ankylosis

This condition would seem to be an obvious stratagem if sutures represented weak points in a turtle shell, and yet it is rather rare. The most familiar example is *Terrapene*, in which loss of carapacial sutures with maturity is typical of at least some subspecies. Perhaps it correlates with a full hinged plastron that, by elimination of the bony bridges, prevents the arch of the carapace having the resistance to crushing afforded by a strong tension member spanning the base of the arch. Generalized carapacial ankylosis is not shown by all box turtles, but interestingly it does appear in adult specimens of the batagurine species *Cistoclemmys galbinifrons*. It may occur occasionally in *Kinosternon bauri*, which also has an extensively hinged plastron although a rigid bridge is present in this taxon.

BRAMBLE (1974) has argued that almost all turtles with well-developed plastral hinges tend to be amphibious or aquatic, with the exception of the majority of species of *Terrapene*. He pointed out the paradox that, while plastral kinesis is a clear advantage to a terrestrial turtle, it involves modifications of the attachments for the limb girdles with the shell that significantly reduce the weight--bearing efficiency of these attachments — a function that is especially important in terrestrial species that are constantly subject to gravitational forces. Such forces would obviously have the least impact in a very small turtle, and it may thus be significant that *Terrapene* is typically smaller than almost any testudinid. The early fusion of all shell bones in *Terrapene* may reflect the need to curtail unnecessary growth once maturity is reached in these very long-lived turtles.

The only living testudinids with more than a rudimentary degree of plastral kinesis, namely certain subspecies of *Pyxis arachnoides* (BOUR, 1981) are, significantly, also among the smallest of tortoises, and the plastral hinge, being further forward than that of hinged emydids (VUILLEMIN and RABODOMIHA-MINA, 1968), may require fewer compromising modifications of the girdles and weight-bearing mechanisms.

Carapacial sutures may be lost in old *Dermatemys* or *Batagur*, and both shell and skull sutures disappear in the extremely thin-shelled, now extinct Mascarene tortoises of the genus *Cylindraspis*. Since in this case ankylosis extended to the skull as well as to the shell, it may derive from some obscure physiological cause rather than from a simple attempt at strengthening the shell. Indeed,

as ARNOLD (1979) points out, a thin, sutureless shell may have some of the same liabilities as the shell of an egg, namely a tendency to be subject to uncontrolled cracks that fracture the entire structure, rather than ending at a point where a sutural line is reached.

Some apparently random fusion of shell elements may occur in trionychids, this tendency being perhaps most marked in *Cyclanorbis elegans* (P. MEYLAN, pers. comm.).

5. Tetragonal neurals

In this condition, the overall neuro-pleural suture lines may be virtually straight. It would seem to offer few mechanical advantages over a more inter-locking structure. This condition occurs in certain extremely flat-shelled turtles such as *Platysternon* and *Trionyx subplanus*, in which there is really no cara-pacial arch to be stabilized by neurals of a more standard configuration, and indeed where some slight neuro-pleural kinesis may occur, especially in *T. sub-planus*, to accommodate the visceral volume changes associated with total retraction of the very large head.

6. Elimination of neural bones in the posterior part of the series

This condition may arise from one of several factors. It occurs in certain relatively large river turtles, such as *Podocnemis*, *Dermatemys*, and *Trionyx*, in which the construction of the pelvic and posterior carapacial area may be extremely different, but in all of which a powerful swimming action is generated by alternating thrusts of the hindlimbs. In such species, the swimming action presumably creates asymmetrical stresses upon the pelvis and posterior cara-pacial area, which may be accommodated or resisted by allowing the pleural bones in this area to have a median connection rather than be separated by intervening pleurals or suprapygals.

This interpretation achieves a modest degree of corroboration from the obser-vation that among the members of the genus *Pseudemys* the neural series is complete, with the exception of the condition in the most powerful swimmer in this group, *P. concinna suwanniensis*, in which the posterior neurals may have a median line of contact. Another intrageneric example is that of *Pelusios*, in which neurals are very variable but in which they are fewest (seven or fewer) in the largest and perhaps strongest-swimming species, *P. sinuatus*. Moreover, within this species, individuals from the very large Lake Tanganyika, which reach a larger body size than the species elsewhere and probably have the most developed swimming ability, have only four or five neurals (BROADLEY, 1983), with reduction occurring at the rear of the series. Also, among the trionychids, the small *Trionyx subplanus*, a relatively poor swimmer, is almost unique in the family in having a complete neural series, with all pleural pairs separated. Even

the pond-dwelling, unstreamlined *Lissemys* has the posteriormost pleurals in median contact. This may be because this species, having raisable semilunar femoral flaps, shows some of the morphological characteristics of box turtles, which often lose posterior neurals for reasons discussed below. This pleural configuration in *Lissemys* could also reflect that this is an advanced rather than primitive form that retains this aspect of its fluviatile, typical trionychid ancestry. Arguments for considering *Lissemys* to be a derived rather than a primitive trionychid are presented by PRITCHARD (1984).

Posterior neurals are also lost in *Caretta*. This may again be related to asymmetrical stresses in the pelvic area, though in this case they are associated with terrestrial locomotion rather than swimming — the hindlimbs serve more as rudders than as thrusters during swimming in cheloniids. In the similar--size cheloniid *Chelonia*, the terrestrial gait differs from that of *Caretta* in that it involves symmetrical thrusts of all four flippers, and in this genus the neural series is complete.

Two other circumstances may also precipitate reduction of the posterior neurals and the anterior suprapygal, so that some posterior pleural pairs become contiguous. Several lineages of turtles have independently developed moveable plastral lobes. Such groups include *Kinosternon*, *Terrapene*, *Cuora*, and their allies. In each of these genera, the pelvis swings forward ventrally to facilitate the enhanced retraction of the hindlimbs. The hinging-point for this swinging action is the dorsal seat of the pelvis, specifically where the ilia rest against the underside of the eighth pleural bones. The hinging-forward action is most effective if the fulcrum is posteriorly placed, and this results in a postero--mesial migration of the contact points on the eighth pleurals that effectively displaces or eliminates the anterior suprapygal and brings the posteriormost pleurals into median contact. Moreover, in turtles with hinged plastra, the plastral lobes are often raised with considerable force (especially when the plastral lobes are large as in *Terrapene* or *Cuora* rather than small as in *Staurotypus*, *Sternotherus*, or *Kinosternon herrerai* — BRAMBLE et al., 1984), presumably to thwart the efforts of a predator bent upon prising the turtle open. Such predatory efforts would place considerable downward force upon the sacral area of the shell via tension on the testoiliacus muscle (BRAMBLE, 1974). An effective modification of the bony mosaic of the sacral part of the carapace to provide resistance to this tension is enlargement of the eighth pleural bones and elimination of the anterior suprapygal, as well as a general narrowing and increased convexity of this area of the carapace.

The posteriormost pleurals are also in median contact, excluding certain neurals, in almost all pleurodires, though some specimens of *Pelusios* are known in which the neural series is complete (BROADLEY, 1981). This seems to be associated with the unique structure of the pleurodiran pelvis, in which each innominate bone forms a distinct, stout pillar bracing the posterior separation of the carapace and plastron. The ventral seat of each of these pillars, formed by the

ischia and pubes, forms two characteristic, non-parallel linear scars on the visceral surface of each side of the plastron. Dorsally, the attachment of the ilia and the seventh and eighth pleural bones is strengthened by a mushroom-like broadening of the top of the ilia, which abut against large, irregularly-shaped scars on each side. Phylogenetic broadening of the contact points between the ilia and the posteriormost pleurals, to the point at which they are almost mesially contiguous, appears to have caused a concomitant mesial migration of the proximal edge of these pleurals, resulting in the displacement of the anterior suprapygal and sometimes the posteriormost neural also. One species, *Podocnemis lewyana*, which is not only a pleurodire but also an extremely fast swimmer, and thus qualifies for posterior neural reduction on two counts, is unique among living turtles in having lost the suprapygals as well as the posteriormost neurals (NICÉFORO MARIA, 1952; WOOD, 1979), the eighth pleurals having become enlarged to a triangular form with a continuous median line of contact, and the sixth and seventh neurals also showing a median line of contact.

All turtles with sideways-retracted necks, i. e. all pleurodires, have the pelvis modified in the manner described above, and no other living turtles do. A functional interpretation of the correlation of these features is not immediately obvious. Possibly the answer lies in the very flat shell that is made possible by retraction of the neck in a horizontal plane rather than by the vertical sigmoid flexure typical of cryptodires. Such flatness may present certain ecological advantages in aquatic streamlining or in facilitating concealment in bottom substrates, but a corresponding disadvantage is the loss of the strong arch from which the typical cryptodire shell gains much of its strength. A substitute means of resistance to vertical pressure or impact is offered to some extent by hypertrophied plastral buttresses, but an additional and valuable resistance to vertical crushing is offered by the pleurodiran twin-pillar type pelvis. BRAMBLE and HUTCHISON (1981) argued that the pleurodire pelvic condition "automatically precludes any form of kinesis involving the posterior half of the plastron", but this conclusion is not absolutely correct. In several chelids (see PRITCHARD and TREBBAU, 1984, for examples), the carapace is attached to the plastron at the bridges by ligamentous tissue only, and although there is no hinging action within the plastron, the plastron as a whole can be tilted slightly in a manner that depresses the posterior lobe, presumably to facilitate the passage of rather large eggs by relatively small species such as *Platemys platycephala*. In such species, the anterior plastral buttresses are well developed but the posterior ones strikingly reduced, and the expanded dorsal ends of the ilia press against, but are not ankylosed to, the sacral region of the carapace.

Actually, the fusion of the pelvis to the shell may be the primitive condition for turtles — it was already shown by the Jurassic species *Platychelys oberndorferi* (BRÄM, 1965), and the pelvis may have become moveable in cryptodires as a modification associated with vertical retraction of the neck.

7. Loss of most or all of the neural bones

This condition occurs exclusively in pleurodires. Although unknown in living pelomedusids, it occurs in the extinct *Eusarkia* and in *"Podocnemis" venezuelensis* (WOOD and DIAZ de GAMERO, 1971; MŁYNARSKI, 1976), while among living chelids it is a common condition, almost universal among the Australasian representatives (RHODIN and MITTERMEIER, 1977), and common also among the South American representatives (PRITCHARD and TREBBAU, 1984). Many chelids have especially long necks, which are thrust laterally with considerable force during feeding. Possibly the asymmetrical stresses imparted upon the vertebral area during such thrusts have resulted in strengthening of the bony mosaic in this area by loss of neural elements. It should be remembered that loss of the neural bones, the keystones of the neural arch, may stabilize the shell against internal stresses such as those associated with feeding, but the development of a median suture running almost the length of the carapace may not constitute a corresponding stabilization against external stress, as during predation. Loss of the keystone would indeed seem to be a mechanical liability, and one that has been countered by other means such as the development of extensive plastral buttresses, and the pleurodiran pelvis.

Why *Chelodina oblonga*, alone in its genus, should always have several neural bones, is not immediately clear. This species may have been isolated from other members of the genus for a great length of time, and the retention of most of the neurals may reflect an alternative to the buttressing of the shell shown by many other pleurodires. This is a very thin-shelled form with the longest neck of any living turtle species.

8. Overall widening of the neural bones

This condition occurs in certain long-necked cryptodires, such as *Emydoidea*, *Deirochelys*, and *Chelydra*. It appears to be correlated with the need to make space for the hypertrophied longissimus dorsi muscles associated with the harpoon-like feeding strike. These enlarged muscles require an increase in the volume of the channel between the dorsal vertebral centra and the point of insertion of the ribs into the pleural bones, which occurs both by a downcurving of the proximal part of the rib heads, and an increase in the longitudinal separation of the lines of insertion of the ribs into the pleural bones on each side of the shell. Such wide neurals do not necessarily make for an increase in the overall strength of the carapacial mosaic, but this liability is compensated, in part, in *Chelydra* by the broadened rib heads with their strong attachments to the dorsal centra, in part by extraordinarily complex and interdigitating sutures between the neural and pleural bones. *Emydoidea* and *Deirochelys*, on the other hand, have developed resistance to vertical crushing of the shell by increasing the convexity of the carapace.

Among pleurodires, *Chelus* has conspicuously broadened neurals, although even in this form the posteriormost neurals usually show median contact, demonstrating the independent causes of elimination of neurals at the rear and in other parts of the carapace. In *Chelus*, the longissimus dorsi are so hypertrophied, and the rib heads so far apart, that elimination of the neurals may not have been feasible, and this area of the carapace is stabilized instead by extremely developed, massive rib heads broadly sutured with the dorsal vertebrae, and very complex, interpenetrating sutures between the neurals and pleurals.

9. Longitudinal or transverse division of neural bones

The frequent transverse and occasional longitudinal division of neural bones is, among living turtles, only found in *Lepidochelys* (PRITCHARD, 1969 b), although this condition is also reported in the extinct cheloniids *Glyptochelone* and *Procolpochelys* (ZANGERL and TURNBULL, 1955; ZANGERL, 1969). ZANGERL also included *Caretta* in this category, but I interpret the neural configuration in this genus as more accurately allocable to Condition 10. The adaptive significance of this condition is not clear. Possibly the additional bones in some way reinforce the neural ridge against impact-stress transmitted through the pleural bones during the unique nest-closing in this genus, wherein the sides of the shell are alternately thumped against the substrate with considerable force. However, another possibility is that the additional neurals have no significance in adult *Lepidochelys*, but that they have significance in juveniles, which have strongly tuberculate carapaces. A separate and additional neural may be involved in providing the bony tip to each of these neural tubercles, comparable to the condition in the extinct marine toxochelyids *Prionochelys* and *Ctenochelys*, in both of which genera the tubercles were very well developed (ZANGERL, 1953), although ZANGERL considered these additional neural elements to be discrete epithecal ossifications, of different ontogenetic origin to the "true" neurals.

10. Neurals reduced in size, kite-shaped and separated by pleurals

In this condition, the neurals in at least part of the series are somewhat reduced in size and often in number, and may be kite-shaped rather than coffin--shaped. There are repeated interruptions of the neural series by opposite pleurals. This condition occurs in a number of unrelated turtles, including *Carettochelys insculpta*, *Phrynops gibbus*, *Pelusios sinuatus*, *Cyclanorbis senegalensis*, *Caretta caretta "gigas"*, and *Dermatemys mawi*. It was also found in one of five *Chelodina rugosa* examined. Several interesting points emerge here. First, the turtles are all unrelated — the species mentioned represent six different families and both suborders of living turtles. This would seem to eliminate any major taxonomic significance of this condition, and is one more example

of the extensive parallel evolution shown by the *Testudines* (ZANGERL, 1969). Furthermore, in each case the closest relatives of the form with this neural condition do not show it. *Carettochelys insculpta* and *Dermatemys mawi* are of course the sole living members of their respective families, but the extinct relatives of these species, namely the anosterine carettochelyids or the adocine dermatemyids, do not show the condition (MŁYNARSKI, 1976), nor do most other species of the genus *Phrynops* (PRITCHARD and TREBBAU, 1984), or *Pelusios* (BROADLEY, 1983), most Atlantic specimens of *Caretta* (ZANGERL and TURNBULL, 1955), or *Cyclanorbis elegans* (LOVERIDGE and WILLIAMS, 1957).

The neural configuration is also very variable within a taxon, and many specimens of all of the above forms do not show this condition. The simplest explanation is that Condition 10 is an evolutionarily transitional situation, perhaps offering greater resistance to certain stresses than the original uninterrupted series of neurals, but less than the "ultimate", or neural-free condition.

11. Anterior displacement of neurals, and fusion of neurals I and II

This condition is typical of trionychids. In these turtles, the characteristic mode of feeding involves fast forward trikes with the extremely long neck (PRITCHARD, 1984). The "reach" of the long neck is enhanced by forward displacement of the joint between the eighth cervical and the first dorsal vertebra, which in *Chitra* is actually near the anterior margin of the nuchal bone (MEYLAN, 1984). The displacement is associated with marked shortening (but not narrowing) of the nuchal bone, and a major anterior displacement of the anterior neurals. Neural I has become foreshortened as it was squeezed between the nuchal and neural II, and in many trionychids it actually fuses with neural II (SMITH, 1931; MEYLAN, 1984). Several of the anterior neurals have migrated so far forward that they only maintain tenuous connections with the pleural pair to which they originally corresponded. Such neurals, hexagonal in shape and with the short sides posteriorly, mimic those of *Rhinoclemmys* or *Kinosternon* etc. (Condition 1), but they differ in that the shape resulted, not from a posterior displacement of a fraction of the length of an individual neural, but from an anterior displacement of almost an entire neural bone.

At a variable point towards the rear of the series, trionychid neurals "switch over" from hexagonal-P to hexagonal-A through the intermediary of a rectangular element. It could be argued that the neurals behind this point have moved forwards by one entire place in the series. The neural series in trionychids has thus not only been "pulled forward" by the anterior migration of the cervico--dorsal articulation, it has received an even stronger "push" from behind. This is probably associated with provision for the extensive flexible "flap" at the rear of the trionychid carapace (presumably helpful when the animal settles or burrows into subaquatic substrates), and the unusually anterior position of the posterior limbs, which generate their kicking thrust near the center of gravity of the trionychid body, and whose position has required a correspon-

ding displacement of the pelvis, the sacral vertebrae, and thus the dorsal vertebrae and neural bones also.

The extreme posterior of the trionychid carapace is very reduced and exceedingly variable even within a species (WEBB, 1961; ATATÜR, 1979), with tendencies towards elimination not only of the posteriormost neurals, but also the supracaudals and even the eighth pleurals.

It is common for some cheloniids (e. g. *Chelonia, Eretmochelys, Natator*) to show either transverse division or anteroposterior compression (it is not entirely obvious which) of the anterior neural bones. In contrast to trionychids, these species have very short necks, but for very different reasons (mainly associated with the need for streamlining and elimination of the anterior "overhang" of the carapace) they may have undergone an anterior displacement of the anterior dorsal vertebrae and neural bones.

IV. CONCLUSIONS

The primitive neural bone configuration for the Order *Testudines* may be assumed to be an unbroken series of about eight elements of moderate width, the first tetragonal and contacting the nuchal bone and the remainder hexagonal-A in shape and the last contacting the anterior suprapygal. This assumption is based upon the presence of such a configuration not only in very diverse and unspecialized extant turtle species, but also in many of the earliest fossil turtle families.

The neural series may be increased in overall breadth in species in which the carapace as a whole is either highly domed or very wide. This derives from purely spatial reasons, widened neurals participating with the pleurals in bridging an increased span between the sides of the shell. The neurals also widen in those species with hypertrophied neck-retraction musculature; such muscular development increases the lateral separation of the free rib-heads and their associated pleural bones, which again leaves an increased distance to be spanned by the neural bones.

The neural series becomes narrower in large, streamlined, relatively small--headed forms (some cheloniids, dermatemyids, carettochelyids, the larger batagurines) presumably because the shell as a whole is narrower in such species, and because the small head and relatively short neck correspond to relatively modest development of the longissimus dorsi musculature.

The neural series may become interrupted by contiguous pairs of pleural bones, or even disappear altogether, in species in which the central region of the shell is subject to powerful or asymmetrical stresses. Thus, in many chelids, in which the neck is thrust or retracted laterally, the neurals are rudimentary or lacking. Also, the posterior neurals disappear in some of the larger and faster freshwater species, in which the swimming thrust is developed with alternating strokes of the hind limbs.

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The special stresses on the carapace associated with hinging of the plastron also tend to result in elimination of the posterior neural bones, and to a lesser extent the anterior neurals (at least in *Pelusios* and *Kinosternon*).

The neural series as a whole may shift backwards, to a primarily 6P rather than 6A configuration, in species in which the neck is retracted deep into the shell; or it may shift drastically forward, compressing neural II into neural I but also producing 6P anterior neurals, in trionychids, in which the head and neck can reach unusually far forward.

Several factors can promote the appearance of octagonal neurals, but generally they form by simple enlargement of certain individual elements subject to special stresses. Thus, the neurals underlying the apices of the (often slightly convex) vertebral scutes of dome-shelled tortoises can resist downward pressure better by transmitting such pressure to each of three, rather than two, pleural bones on each side. The neural bones that overlie the neck-suspensory area in big-headed species, or which underlie the high carapace tubercle in *Kachuga*, also tend to become octagonal, for similar reasons. But an octagonal neural may also represent simply a transition between anterior 6A (or 4) and posterior 6P elements.

The striking differences in neural bone configuration observed between turtles of different form or behavior, but on the other hand the clear existence of an "archetypal" configuration for almost any individual species, argue strongly that different neural bone configurations are highly adaptive and play a major role in shell architecture and stress resistance. On the other hand, the frequent deviations from the archetype observed in many turtle species, uncorrelated with any apparent loss in fitness, suggest that the selective pressure to maintain the archetypal configuration is not particularly strong, and survival to maturity of an individual turtle depends upon many factors more critical than its neural bone configuration, good luck being perhaps the most important factor of all.

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REFERENCES

ARNOLD E. N. 1979. Indian Ocean giant tortoises: their systematics and island adaptations. Phil. Trans. Roy. Soc. London, B, **286**: 127—145.

ATATÜR M. K. 1979. Investigations on the morphology and osteology, biotope and distribution in Anatolia of *Trionyx tringuis* (*Reptilia, Testudines*) with some observations on its biology. Ege Univ. Fen Fak. Monogr. Ser., **18**: 1—75.

AUFFENBERG W. 1976. The genus *Gopherus* (*Testudinidae*): Pt. 1. Osteology and relationships of extant species. Bull. Florida State Mus., Biol. Sci., Gainesville, **20**: 47—110.

BERRY J. F., LEGLER J. M. 1980. A new turtle (genus *Kinosternon*) from northwestern Mexico. Contr. Sci. Nat. Hist. Mus. Los Angeles County, 325: 1—12.

BOULENGER G. A. 1889. Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum (Natural History). Taylor and Francis, London, 311 pp.

BOUR R. 1973. Contribution à la connaissance de *Phrynops nasutus* (SCHWEIGGER: 1812) et *Phrynops tuberculatus* (LUEDERWALDT: 1926). Description d'une nouvelle sous-espèce originaire du Paraguay, *Phrynops tuberculatus vanderhaegei* (*Testudinata-Pleurodira--Chelidae*). Bull. Soc. Zool. France, Paris, 98: 175—190.

BOUR R. 1981. Etude systématique du genre endémique malgache *Pyxis* BELL, 1827 (*Reptilia, Chelonii*). Bull. Mens. Soc. Linn. Lyon, 50 (4—5): 132—176.

BOUR R. 1984. Les tortues terrestres géantes des îles de l'océan indien occidental: données géographiques, taxonomiques et phylogénétiques. Studia Geol. Salmant., Salamanca, vol. esp. 1 (Studia Palaeochelonol. 1): 17—76.

BOUR R. 1986. Note sur *Pelusios adansonii* (SCHWEIGGER, 1812) et sur une nouvelle espèce affine du Kenya (*Chelonii, Pelomedusidae*). Studia Palaeocheloniol., Salamanca, 2: 23—54.

BOURRET R. 1941. Les tortues de l'Indochine. Inst. Océanographique de l'Indochine, Cauda, 38: 1—235.

BRÄM H. 1965. Die Schildkrötenresten aus dem Oberen Jura (Main) der Gegend von Solothurn. Mém. Suiss. Paléont., Zürich, 83: 1—190.

BRAMBLE D. M. 1974. Emydid shell kinesis: biomechanics and evolution. Copeia, Ann Arbor, 1974: 707—727.

BRAMBLE D. M., HUTCHISON J. H. 1981. A reevaluation of plastral kinesis in African turtles of the genus *Pelusios*. Herpetologica, Lawrence, 37 (4): 205—212.

BRAMBLE D. M., HUTCHISON J. H., LEGLER J. M. 1984. Kinosternid shell kinesis: structure, function, and evolution. Copeia, Ann Arbor, 1984: 456—475.

BROADLEY D. G. 1981. A review of the genus *Pelusios* WAGLER in southern Africa (*Pleurodira: Pelomedusidae*). Occas. Pap. Natl. Mus. Rhodesia, B (Nat. Sci.), Bulawayo, 6 (9): 633—686.

BROADLEY D. G. 1983. Neural pattern — a neglected taxonomic character in the genus *Pelusios* WAGLER (*Pleurodira: Pelomedisidae*). In: A. RHODIN, K. MIYATA (eds): Advances in herpetology and evolutionary biology. Essays in honor of Ernest E. WILLIAMS. Mus. Compar. Zool., Harvard Univ., Cambridge, pp. 159—168.

BURBIDGE A. A. 1967. The biology of south-western Australian tortoises. Ph. D. thesis, Univ. Western Australia, Nedlands.

BURBIDGE A. A., KIRSCH J. A. W., MAIN A. R. 1974. Relationships within the Chelidae (*Testudines: Pleurodira*) of Australia and New Guinea. Copeia, Ann Arbor, 1974: 392—409.

CARPENTER K. 1981. Preneural in the evolution of *Trionyx*. Copeia, Ann Arbor, 1981: 456—457.

COKER R. E. 1910. Diversity in the scutes of *Chelonia*. J. Morphol., Philadelphia, 21: 1—75.

COPE E. D. 1865. Third contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia, 17: 185—198.

CRUMLY R. R. 1984. The evolution of land tortoises (family *Testudinidae*). Ph. D. Dissertation, Rutgers University, Newark, 584 pp.

DERANIYAGALA P. E. P. 1939. The tetrapod reptiles of Ceylon, vol. 1. Testudinates and crocodilians. Colombo Mus., Colombo, 412 pp.

DOBIE J. R. 1981. The taxonomic relationship between *Malaclemys* GRAY, 1844 and *Graptemys* AGASSIZ, 1857 (*Testudines: Emydidae*). Tulane Stud. Zool. Bot., New Orleans, 23: 85—102.

ERNST C. H. 1978. A revision of the neotropical turtle genus *Callopsis* (*Testudines: Emydidae: Batagurinae*). Herpetologica, Lawrence, 34: 113—134.

ERNST C. H. 1985. *Platemys*, *Platemys platycephala* (*Reptilia: Testudines: Chelidae*). Cat. Amer. Amph. Rept.

ERNST C. H., GIBBONS J. W., NOVAK S. S. 1985. *Chelydra* (*Reptilia: Testudines: Chelydridae*). Cat. Amer. Amph. Rept.

GADOW H. 1899. Onthogenetic variation in the shells of *Chelonia*. Willey's Zool. Results, III, pp. 207—222.

GÜNTHER A. C. L. G. 1877. The gigantic land-tortoises (living and extinct) in the collection of the British Museum. Brit. Mus. (Nat. Hist.), London, 96 pp.

HUMMEL K. 1929. Die fossilen Weichschildkröten (*Trionychia*). Geol.-Paläont. Abh., N. F., Berlin—Jena, **16**: 359—487.

IVERSON J. B. 1981. Biosystematics of the *Kinosternon hirtipes* species group (*Testudines*: *Kinosternidae*). Tulane Stud. Zool. Bot., New Orleans, **23**: 1—74.

LEGLER J. M. 1965. A new species of turtle, genus *Kinosternon*, from Central America. Univ. Kansas Publ. Mus. Nat. Hist., Lawrence, **15**: 615—625.

LEGLER J. M., CANN J. 1980. A new genus and species of chelid turtle from Queensland, Australia. Contr. Sci. Nat. Hist. Mus. Los Angeles County, **324**: 1—18.

LOVERIDGE A., WILLIAMS E. E. 1957. Revision of the African tortoises and turtles of the suborder *Cryptodira*. Bull. Mus. Compar. Zool., Cambridge, **115**: 163—557.

McDOWELL S. B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic *Testudinidae*. Proc. Zool. Soc., London, **143**: 239—279.

McBEE K., BICKHAM J. W., RHODIN A. G. J., MITTERMEIER R. A. 1985. Karyotypic variation in the genus *Platemys* (*Testudines*: *Pleurodira*). Copeia, Ann Arbor, **1985**: 445—449.

MEYLAN P. 1984. Evolutionary relationships of recent trionychid turtles: evidence from shell morphology. Studia Geol. Salmant., Salamanca, vol. esp. **1** (Studia Palaeocheloniol. **1**): 169—188.

MEYLAN P., AUFFENBERG W. 1986. New land tortoises (*Testudines*: *Testudinidae*) from the Miocene of Africa. Zool. J. Linn. Soc., London, **86**: 279—307.

MILSTEAD W. 1969. Studies on the evolution of box turtles (genus *Terrapene*). Bull. Florida State Mus., Biol. Sci., Gainesville, **14**: 1—113.

MŁYNARSKI M. 1969. Fossile Schildkröten. A. Ziemsen, Wittenberg, 128 pp.

MŁYNARSKI M. 1976. *Testudines*. Handbuch der Paläoherpetologie, Part **7**. Gustav Fischer, Stuttgart, 130 pp.

NEWMAN H. H. 1906. The significance of scute and plate „abnormalities" in *Chelonia*. Biol. Bull., **10**: 86—114.

NICÉFORO MARIA H. 1952. Testudineos del suborden *Pleurodira* en el Museo de la Salle. Bol. Inst. La Salle, Bogotá, **39**: 1—8.

OBST F. J. 1982 (1983). Beitrag zur Kenntnis der Landschildkrötengattung *Manouria* GRAY, 1852. Zool. Abh. Staatl. Mus. Tierkunde, Dresden, **38**: 247—256.

OBST F. J., MEUSEL W. 1978. Die Landschildkröten Europas, 2nd ed. Die Neue Brehm-Bücherei. A. Ziemsen Verlag, Wittenberg, 72 pp.

PARKER G. H. 1901. Correlated abnormalities in the scutes and bony plates of the carapace of the sculptured tortoise. Amer. Nat., Salem, **35**: 17—24.

PRITCHARD P. C. H. 1969a. Herrera's mud turtle. Internat. Turtle Tortoise Soc. J., Los Angeles, **3** (3): 6—9, 35.

PRITCHARD P. C. H. 1969b. Studies of the systematics and reproductive cycles of the genus *Lepidochelys*. Ph. D. Dissertation, Univ. Florida, 197 pp.

PRITCHARD P. C. H. 1984. Piscivory in turtles, and evolution of the long-necked *Chelidae*. In: M. W. J. FERGUSON (ed.): The structure, development, and evolution of reptiles. Zool. Soc. London Symp., London, No. 52, pp. 87—110.

PRITCHARD P. C. H., TREBBAU P. 1984. The turtles of Venezuela. Soc. Study Amph. Rept., Spec. Publ. No. 2, 403 pp.

PROCTER J. 1922. A study of the remarkable tortoise *Testudo loveridgei* BLGR., and the morphology of the chelonian carapace. Proc. Zool. Soc., London, **34**: 483—526.

RHODIN A. G. R., MITTERMEIER R. 1977. Neural bones in chelid turtles from Australia and New Guinea. Copeia, Ann Arbor. **1977**: 370—372.

RHODIN A. G. R., MITTERMEIER R. 1983. Description of *Phrynops williamsi*, a new species of chelid turtle of the South American *P. geoffroanus* complex. In: A. RHODIN, K. MIYATA (eds):

Advances in herpetology and evolutionary biology. Essays in honor of Ernest E. WILLIAMS. Mus. Compar. Zool., Harvard Univ., Cambridge, pp. 58—73.

SIEBENROCK F. 1904. Shildkröten von Brasilien. Denschr. Math. -Naturwiss. Kl. Kaiserl. Akad. Wiss., Wien, **76**: 1—28.

SMITH M. A. 1931. The fauna of British India, including Ceylon and Burma. *Reptilia* and *Amphibia*. Vol. **1**, *Loricata, Testudines*. Taylor and Francis, London, 185 pp.

TINKLE D. W. 1958. The systematics and ecology of the *Sternothaerus carinatus* complex (*Testudinata, Chelydridae*). Tulane Stud. Zool. Bot., New Orleans, **6**: 1—56.

TINKLE D. W., WEBB R. G. 1955. A new pecies of *Sternotherus* with a discussion of the *Sternotherus carinatus* compex. Tulane Stud. Zool. Bot., New Orleans, **3**: 53—67.

TRONC E., VUILLEMIN S. 1974. Contribution á l'étude de la faune endémique Malgache: Etude ostéologique de *Erymnochelys madagascariensis* GRANDIDIER, 1867 (Chélonien, *Pelomedusidae*). Bull. Acad. Malagas., **51**: 189—224.

VILLIERS A. 1958. Tortues et crocodiles de l'Afrique Noire française. Init. Afr., Dakar, **15**: 1—354.

VUILLEMIN S., RABODOMIHAMINA L. 1968. Contribution à l'étude de la faune endémique malgache: particularités anatomiques de *Pyxis arachnoides* BELL, 1827 (*Testudinidae*). Ann. Univ. Madagascar (Sci. Nat. Math.), Tananarive, **5**: 79—106.

WARREN J. W. 1969. Chelid turtles from the mid-Tertiary of Tasmania. J. Paleont., Tulsa, **43**: 179—182.

WEBB R. G. 1962. North American Recent soft-shelled turtles (family *Trionychidae*). Univ. Kansas Publ., Mus. Nat. Hist. Lawrence, **13** (10): 429—611.

WILLIAMS E. E. 1953. Fossils and the distribution of chelyid turtles. Breviora, Cambridge, **13**: 1—8.

WOOD R. C. 1971. The fossil *Pelomedusidae* (*Testudines, Pleurodira*) of Africa. Ph. D. Dissertation. Harvard Univ., Cambridge.

WOOD R. C. 1976. Two new species of *Chelus* (*Testudines: Pleurodira*) from the late Tertiary of Northern South America. Breviora, Cambridge, **435**: 1—26.

WOOD R. C. 1979. Studies of the systematics, evolution, and ecology of pleurodiran turtles in South America. Natl. Geogr. Res. Rep., Washington, 1970 projects, pp. 591—599.

WOOD R. C. (ms). A review of the fossil *Chelidae* (*Testudines, Pleurodira*) of South America, with a description of several new occurrences, 28 pp.

WOOD R. C., DIAZ de GAMERO M. L. 1971. *Podocnemis venezuelensis*, a new fossil pelomedusid (*Testudines: Pleurodira*) from the Pliocene of Venezuela, and a review of the history of *Podocnemis* in South America. Breviora, Cambridge, **405**: 1—10.

WOOD R. C., MOODY R. T. J. 1976. Unique arrangement of carapace bones in the South American chelid turtle *Hydromedusa maximiliani* (MIKAN). Zool. J. Linn. Soc., London, **59**: 69—78.

ZANGERL R. 1939. The homology of the shell elements in turtles. J. Morphol., Philadelphia, **65**: 383—406.

ZANGERL R. 1948. The vertebrate fauna of the Selma Formation of Alabama. Part II. The pleurodiran turtles. Fieldiana: Geol. Mem., Chicago, **3**: 17—56.

ZANGERL R. 1953. The vertebrate fauna of the Selma Formation of Alabama. Part IV. The turtles of the family *Toxochelyidae*. Fieldiana: Geol. Mem., **3**: 137—274.

ZANGERL R. 1969. The turtle shell. In: C. GANS, A. d'A. BELLAIRS, T. S. PARSONS (eds): The biology of the *Reptilia*. Morphology A, vol. **1**. Academic Press, London—New York, pp. 311—339.

ZANGERL R., HENDRICKSON L. P., HENDRICKSON J. R. (in press) *Natator depressus* (GARMAN), a redescription of the Australian flatback sea turtle, with notes on its distribution, habitat, and diet. Bishop Museum Press.

ZANGERL R., MEDEM F. 1958. A new species of chelid turtle, *Phrynops* (*Batrachemys*) *dahli*, from Colombia. Bull. Mus. Compar. Zool., Cambridge, **119**: 375—390.

ZANGERL R., TURNBULL W. D. 1955. *Procolpochelys grandaeva* (LEIDY), an early Carettine sea turtle. Fieldiana: Zool., Chicago, **37**: 345—382.

STRESZCZENIE

Neuralia (tarczki kręgowe) w pancerzach żółwi są kośćmi o największej zmienności. Przypuszczalnie pierwotny wzorzec złożony z ośmiu przeważnie sześciokątnych neuraliów ulegał rozmaitym modyfikacjom — zwiększenie liczby neuraliów (maksymalnie do 15); zmniejszenie liczby neuraliów (zwykle w części tylnej pancerza) aż do całkowitego zaniku w skrajnych przypadkach; zmiany kształtu neuraliów przez ich rozszerzenie, zwężenie albo zmniejszenie ich rozmiarów (w formie izolowanych romboidalnych elementów), odwrócenie (w formie sześciokątów z rozszerzonym tylnym bokiem) bądź przyjęcie kształtu występujących na przemian ośmio- i czworokątów. Literatura przedmiotu notuje wiele z wymienionych modyfikacji, choć w sposób niekompletny lub anegdotyczny, brak też przeważnie w literaturze interpretacji funkcjonalnej odmiennych wzorców neuraliów występujących wśród współczesnych żółwi. W niniejszej pracy każdy z podstawowych wzorców neuraliów jest skorelowany z innymi danymi anatomicznymi lub z trybem życia poszczególnych gatunków.

Edited by Dr. Z. Szyndlar