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SEXUAL DIMORPHISM, ALLOMETRY AND VERTEBRAL SCUTE MORPHOLOGY IN *NOTOCHELYS PLATYNOTA* (GRAY, 1834)

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(with four text-figures)

ABSTRACT.– **Sexual dimorphism, allometry, and vertebral scute morphology were studied in the Malayan flat-shelled turtle, *Notochelys platynota* (Gray, 1834). Adult males (mean CL = 238.29 ± 50.68 mm, range 130.5-282.0, n = 16) were, on average, larger than adult females (mean CL = 203.48 ± 52.50 mm, range 125.3-330.0, n = 44). The five largest individuals in the study, however, were females (283-330 mm CL). The SDI value for this species was calculated as -1.17. Sexual dimorphism of the shell was not evident when examined by ANCOVA. The regression slopes of males and females differed significantly ($P < 0.05$) in only one of 26 characters examined. Allometric growth of the shell, however, was evident in *N. platynota*. Shell shape changed as CL increased proportionally more than shell width, shell height and plastral length (18/26 characters). This allometric growth pattern yields adults with relatively narrower and flatter shells than juveniles. Of 127 specimens examined, 3.9% (n = 5) had five vertebral scutes, 85.0% (n = 108) had six, 10.2 % (n = 13) had seven and 0.8% (n = 1) had eight vertebrals. In specimens with five vertebrals (presumably the ancestral condition), all scutes were large, broader than long, and of similar length. In specimens with six or seven vertebrals, the first four and last vertebrals (Vert6 or 7) were large and broader than long. The smaller supernumerary scutes characteristic of this species were usually found between the fourth and last vertebrals and were occasionally longer than broad (5% of specimens, n = 5). The presence of supernumerary scutes does not affect the relative length of the entire vertebral series, as evidenced by a lack of variation in this character among specimens with five, six and seven vertebrals. Instead, as suggested by an increased width to length ratio of several normal scutes in specimens with six or seven vertebrals, there is a shortening of several normal scutes to accommodate the additional ones. In specimens with six or seven vertebral scutes, the relative lengths of most normal vertebrals (all except Vert1) were noticeably shorter than in specimens with five vertebral scutes. The fourth and last (Vert6 or 7) vertebrals were the shortest of these normal scutes.**

KEY WORDS.– **Testudines; Bataguridae; *Notochelys platynota*; allometry; sexual dimorphism; vertebral scute morphology.**

INTRODUCTION

Notochelys platynota (Gray, 1834), the Malayan flat-shelled turtle, is a medium-sized batagurid turtle reaching maximum sizes of 33-36 cm carapace length (Ernst and Barbour, 1989; Lim and Das, 1999; Ernst et al., 2000). This species shows some secondary sexual dimorphism, with males having slightly concave plastra and thicker tails than the flat-plastroned females (Ernst and Barbour, 1989; Ernst et al., 2000). Sexual dichromatism has also been reported in this species. The carapace of males has a buff to yellowbrown ground colour that is irregularly mottled with a darker brown pigment, whereas the carapaces of immature individuals and females are more uniformly olive- to reddish-brown (E. O. Moll, pers. comm.). In addition, the head and neck is often much darker (almost black) in adult males (E. O. Moll, pers. comm.), and the nose of males may show a red colouration during the breeding season (Philippen, 1988). Populations of *N. platynota* can be found in clear streams and small rivers, often fast flowing and usually in forested areas (Moll and Khan, 1990; Lim and Das, 1999), from peninsular Thailand southward through Malaysia, Sumatra, and Java to Borneo (Ernst and Barbour, 1989; Ernst et al., 2000). This species is unique in typically having more than five vertebral scutes (usually six or seven). These additional scutes have symmetrical connections with the adjacent pleural scutes and a definite position in the vertebral series (Ernst and Barbour, 1989; Ernst et al., 2000).

Sexual dimorphism and allometry of the turtle shell have been studied extensively (see Mosimann, 1956; Berry and Shine, 1980; Ernst and Lovich, 1986; Gibbons and Lovich, 1990; Ernst et al., 1998 for reviews). Both are important factors in studies of ecology, physiology, nutrition, embryology, morphogenesis, evolution, and taxonomy (Mosimann, 1958; Berry and Shine, 1980; Gibbons and Lovich, 1990). Sexual dimorphism and allometry are particularly important to taxonomy because a detailed investigation of intrapopulational variation is a crucial first step in any study of interpopulational differences. Without such considerations, critical errors in taxonomic judgment are likely to occur.

The purpose of this paper is to examine sexual dimorphism, allometry and vertebral scute morphology in *N. platynota*. Although these aspects have been studied widely in turtles, little attention has been focused on this species. In fact, we are not aware of any previous study that quantifies these for *N. platynota*. *Notochelys platynota* is listed as vulnerable (VU A1cd+2cd) on the 2000 IUCN Red List and is perhaps one of the least known semi-aquatic turtles in all of tropical Asia (Buskirk, 1997). This study is, therefore, an important contribution to the biological understanding of this species.

MATERIALS AND METHODS

We examined museum specimens from throughout the known range of *Notochelys platynota*. Dial calipers (accurate to 0.1 mm) were used to take the following 29 straight-line measurements on the shell of each specimen (see Ernst and Lovich, 1986): maximum carapace length (CL); carapace width at the level of the seam separating vertebral scutes 2 and 3 (CW); shell height at the level of the seam separating vertebral scutes 2 and 3 (SH); maximum plastron length (PL); maximum width (APLW and PPLW) and length (APLL and PPLL) of both plastral lobes; minimum bridge length (BrL); maximum width and length of vertebral scutes 1-7 (Vert1-7W and L); and medial seam length of all plastral scutes (GulL, HumL, PecL, AbdL, FemL, and AnL). The condition of bilateral characters was recorded from the right side of the carapace and the left side of the plastron unless damaged. Museum abbreviations followed Leviton et al. (1985) and Leviton and Gibbs (1988) with the following additions: KUZ = Kyoto University Zoological Collection, Kyoto, Japan; WPM = personal collection of William P. McCord, Hopewell Junction, New York, USA; ZRC = Raffles Museum of Biodiversity Research, Zoological Reference Collection, The National University of Singapore, Singapore.

Tail morphology and plastral concavity were the primary characteristics used for sexual identification in this study. Males have slightly concave plastra and thicker tails than do the flat-plastroned females (Ernst and Barbour, 1989; Ernst et al., 2000). When tail morphology was not available (shell and skeletal material; some dried specimens), information from museum records sometimes formed the basis of sexual identification. All specimens examined were preserved or skeletal, so carapace colour and pattern were not always discernable.

To test for sexual dimorphism, CL was used as the independent variable for regression analyses (least squares method) of other shell characters. Nontransformed data (mm) were utilized for all specimens that had a determinable sex, and males and females were analyzed separately. The regression slopes of each bivariate relationship were compared for males and females using Analysis of Covariance (ANCOVA), with CL as the covariate and sex as the fixed factor. Significantly different slopes ($\alpha = 0.05$) indicated sexual dimorphism in the characters regressed against CL (Mosimann and Bider, 1960; Mouton et al., 2000). In addition, sexual differences in CL were tested using Student's t-test and expressed by the sexual dimorphism index (SDI) proposed by Gibbons and Lovich (1990), which is calculated as follows: +f/m when f > m; or –m/f when f < m, where 'f' and 'm' denote mean CL for adult females and males, respectively. To minimize the effects of allometric growth, only specimens > 125 mm CL were utilized in these last two analyses. For the t-test, the Kolmogorov-Smirnov test was used to verify normality and an F-test was used to compare variances.

To test for allometric variation, CL was again used as the independent variable for regression analyses (least squares method) of other shell characters. Nontransformed data (mm) were utilized for all specimens regardless of sex or size. Based on preliminary results regarding sexual dimorphism, all specimens (males, females, and juveniles) were analyzed together. The slope and intercept of each regression equation were tested for differences from zero using Student's t-tests. Intercepts that were significantly different from zero ($\alpha = 0.05$) indicated differential growth (i.e., allometry) of the characters involved (Mosimann, 1958; Stickel and Bunck, 1989).

Several aspects of vertebral scute morphology were also investigated. These included the distribution of vertebral scute number, relative lengths of each vertebral scute and the entire vertebral series, width to length ratios for each vertebral scute, and the position and origin of supernumerary scutes in the vertebral series. To verify the identity of the smaller supernumerary scutes (sometimes referred to as extra or additional scutes), relative lengths of all vertebral scutes (length of scute divided by length of entire vertebral series) were compared in specimens with six or seven vertebrals. The relative lengths of the entire vertebral series (length of entire vertebral series divided by CL) were compared among specimens bearing five, six, and seven vertebral scutes. The width to length ratio of each vertebral scute was also compared among specimens bearing five, six, and seven vertebral scutes. Finally, in an attempt to discover the origin of the extra vertebrals in this species, the relative lengths of each normal vertebral scute (Vert1-4 and last vertebral) were compared among specimens bearing five, six, and seven vertebrals.

When parametric assumptions were met, the statistical comparisons above were made with a one-way ANOVA followed by the Tukey-Kramer multiple comparison test (q). Assumptions of normality and homogeneity of variances were tested using the Kolmogorov-Smirnov and Bartlett's tests, respectively. The Kruskal-Wallis test (KW) followed by Dunn's multiple comparison test (mean rank difference = MRD) was used when parametric assumptions were violated. Significance levels were 0.05 in all cases.

RESULTS AND DISCUSSION

Our data indicated that males were, on average, slightly larger than females. Adult males averaged 238.29 ± 50.68 (mean ± 1 SD) mm CL (130.5-282.0 mm, n = 16), whereas adult females averaged 203.48 ± 52.50 mm CL (125.3-330.0 mm, n = 44). This difference in mean carapace lengths was statistically significant ($t = 2.3$, $df = 58$, $P < 0.05$). It is important to note, however, that the five largest individuals in this study were females (283-330 mm CL). The largest individual recorded in this study (BMNH 95.5.14.4), an adult female from Borneo (330 mm CL), is probably the same specimen reported by Boulenger (1912). The SDI value for *N. platynota*, calculated from these same data, was -1.17. SDI values for the entire turtle order range from -1.45 to +2.10 (Gibbons and Lovich, 1990). When compared to other species that have males as the larger sex (mean SDI = -1.10; median SDI = -1.08), *N. platynota* displayed a slightly more negative than average SDI value (Gibbons and Lovich, 1990). It is difficult to draw any firm conclusions regarding overall size differences between the sexes, however, because of relatively small sample sizes, the imbalance of adult male to female sample sizes, and possible collecting bias between samples.

Sexual dimorphism of the shell was not evident in *N. platynota* when examined by ANCO-

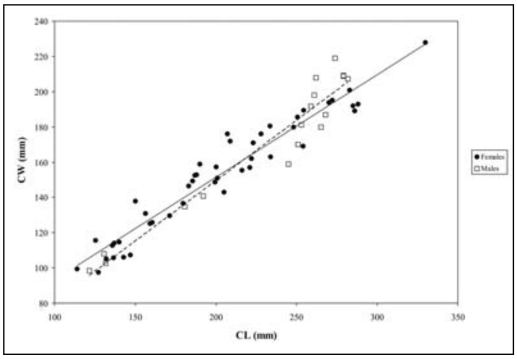

FIGURE 1: Allometry of carapace width plotted as a function of carapace length and sex for *Notochelys platynota* (Female: CW = 35.04 + 0.58CL; Male: CW = 12.43 + 0.68CL; ANCOVA: df = 1,58, F = 4.55, P < 0.05).

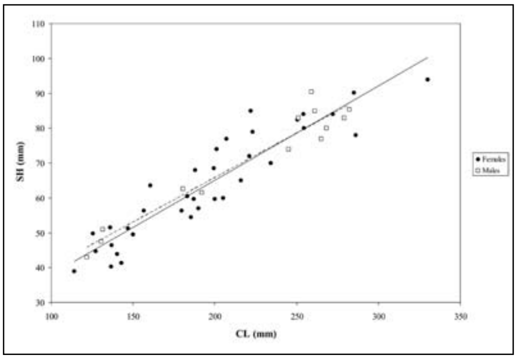

FIGURE 2: Allometry of shell height plotted as a function of carapace length and sex for *Notochelys platynota* (Female: SH = 11.04 + 0.27CL; Male: SH = 14.78 + 0.26CL; ANCOVA: df = 1,44, F = 0.22, ns).

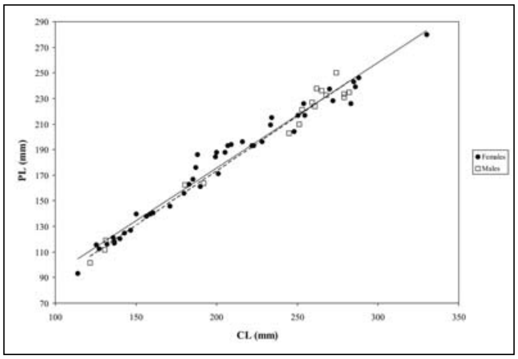

FIGURE 3: Allometry of plastron length plotted as a function of carapace length and sex for *Notochelys platynota* (Female: PL = 10.67 + 0.82CL; Male: PL = 2.61 + 0.85CL; ANCOVA: df = 1,57, F = 0.51, ns).

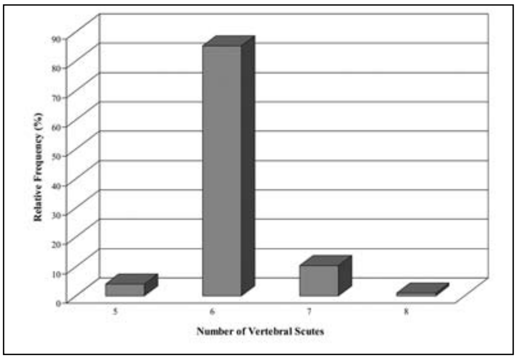

FIGURE 4: Frequency distribution for number of vertebral scutes in *Notochelys platynota* (n = 127).

VA. These analyses indicated that the regression slopes of males and females differed significantly ($P < 0.05$) in only one of the 26 characters examined (Table 1, Figs. 1-3). For CW (Table 1, Fig. 1), the difference in slopes was barely significant ($P > 0.03$). This apparent lack of sexual dimorphism in shell shape may also be due to problems with our sample.

Allometric growth of the shell, however, was evident in *N. platynota* (Table 2). Since very little sexual dimorphism was detected, allometric analyses included all specimens regardless of sex or size. Shell shape changed in this species as CL increased proportionally more than shell width (CW, APLW, PPLW), shell height (SH), plastral length (PL and APLL), and several scute widths (Vert2-6W) and lengths (Vert2-4L, Vert6L, BrL, PecL, AbdL).

Allometry of shell characters is a widespread phenomenon among turtles. The allometric pattern that emerges for *N. platynota* is one where both sexes grow proportionally longer than wider or higher. This allometry yields adults with relatively narrower and flatter shells than juveniles. It is critical to emphasize the interrelatedness of allometric growth and sexual dimorphism (or lack thereof). The similar allometric growth pattern of males and females produces adults that lack sexual dimorphism and have the same general proportions. Such a connection has been demonstrated by other authors working with a variety of turtle species (Mosimann,

TABLE 1: Allometric relationships and comparison of regression slopes (ANCOVA) of shell characters versus carapace length among male and female *Notochelys platynota.* All slopes are significantly ($P < 0.0001$) different from zero. For significance levels, ns = $P > 0.05$.

Character	Sex	N	Linear relation y = a + bx (in mm)	R^2	Male vs. Female Slope (b) (H_o: $b_{males} = b_{females}$)
CW	F	45	CW = 35.04 + 0.58CL	0.93	$F_{1,58}$=4.55, p<0.05
	M	17	CW = 12.43 + 0.68CL	0.93	
SH	F	35	SH=11.04 + 0.27CL	0.86	$F_{1,44}$=0.22, ns
	M	13	SH = 14.78 + 0.26CL	0.93	
PL	F	44	PL = 10.67 + 0.82CL	0.97	$F_{1,57}$=0.51, ns
	M	17	PL = 2.61 + 0.85CL	0.98	
APLW	F	44	APLW = 3.33 + 0.40CL	0.93	$F_{1,57}$=1.05, ns
	M	17	APLW =-5.22 + 0.44CL	0.90	
APLL	F	43	APLL = 4.12 + 0.40CL	0.92	$F_{1,56}$=1.25, ns
	M	17	APLL = -7.39 + 0.44CL	0.91	
PPLW	F	43	PPLW = 1.88 + 0.45CL	0.92	$F_{1,56}$=0.04, ns
	M	17	PPLW =-2.61 + 0.46CL	0.92	
PPLL	F	43	PPLL = 6.77 + 0.43CL	0.95	$F_{1,56}$=0.47, ns
	M	17	PPLL = 1.42 + 0.45CL	0.97	

TABLE 2: Allometric relationships of shell characters to carapace length for *Notochelys platynota.* All slopes are significantly ($P < 0.0001$) different from zero. For significance levels, ns = $P > 0.05$.

Character	N	Linear relation: y = a + bx (in mm)	R^2	Significance levels (P) Intercept (a) (H_0: a = 0)
CW	136	CW= 15.12+ 0.68CL	0.98	< 0.0001
SH	118	SH = 3.02 + 0.31CL	0.96	< 0.001
PL	132	PL = -4.07 + 0.89CL	0.99	< 0.001
APLW	132	APLW = -2.33 + 0.42CL	0.98	<0.01
APLL	131	APLL = -3.85 + 0.43CL	0.98	< 0.0001
PPLW	131	PPLW = -3.78 + 0.47CL	0.98	< 0.001
PPLL	131	PPLL = -0.44 + 0.46CL	0.99	ns
Vert1W	110	Vert1W = 0.14+ 0.24CL	0.93	ns
Vert1L	109	Vert1L = -0.25 +0.17CL	0.97	ns
Vert2W	109	Vert2W = 2.94 + 0.27CL	0.97	< 0.0001
Vert2L	109	Vert2L =-1.31+0.19CL	0.98	<0.01
Vert3W	109	Vert3W=1.53+0.28CL	0.97	<0.05
Vert3L	108	Vert3L = -1.95 + 0.20CL	0.98	< 0.0001
Vert4W	108	Vert4W = -2.76 + 0.27CL	0.97	< 0.001
Vert4L	108	Vert4L =-1.63 +0.16CL	0.94	<0.05
Vert5W	109	Vert5W = -3.46 + 0.19CL	0.90	< 0.001
Vert5L	85	Vert5L = -1.43+0.12CL	0.78	ns
Vert6W	105	Vert6W = -3.55+0.25CL	0.93	< 0.001
Vert6L	104	Vert6L = -4.10 + 0.20CL	0.87	< 0.001
BrL	129	BrL = 3.52 +0.31CL	0.97	< 0.0001
GulL	133	GulL =-0.83+ 0.12CL	0.94	ns
HumL	133	HumL = 0.08 + 0.09CL	0.86	ns
PecL	133	PecL = -1.49 +0.19CL	0.95	<0.05
AbdL	133	AbdL =1.27 +0.17CL	0.96	<0.05
FemL	133	FemL = 0.54 + 0.08CL	0.84	ns
AnL	133	AnL =-1.09+ 0.17CL	0.94	ns

TABLE 3: Relative lengths - mean ± 1 SD (median) - of vertebral scutes 1-7 in *Notochelys platynota.* Values are expressed as a percentage of the total length of all vertebral scutes.

Number Vertebrals	Vert1	Vert2	Vert3	Vert4	Vert5	Vert6	Vert7
5 (n=4)	17.8±1.2 (17.4)	20.4±0.2 (20.3)	20.7±1.0 (20.6)	20.5±2.1 (19.8)	20.6±3.3 (21.5)	-	-
6 (n=95)	17.9±1.3 (17.8)	18.9±1.0 (18.8)	18.8±1.1 (18.7)	15.5±1.2 (15.5)	11.4±1.7 (11.3)	17.5±1.8 (17.6)	-
7 (n=9)	17.7±1.5 (16.9)	18.0±1.2 (18.0)	17.1±1.6 (16.6)	12.9±3.5 (14.0)	9.8±2.1 (9.0)	8.8±2.0 (8.4)	15.8±2.0 (14.5)

TABLE 4: Width to length ratio – mean ± 1 SD (median) – of vertebral scutes 1-7 in *Notochelys platynota*. Values calculated by dividing scute width by scute length.

Number Vertebrals	Vert1	Vert2	Vert3	Vert4	Vert5	Vert6	Vert7
5 (n=4)	1.44±0.23 (1.44)	1.42±0.11 (1.38)	1.44±0.14 (1.49)	1.23±0.18 (1.23)	1.18±0.22 (1.12)	-	-
6 (n=95)	1.40±0.16 (1.40)	1.64±0.18 (1.62)	1.65±0.19 (1.62)	1.65±0.18 (1.63)	1.37±0.25 (1.37)	1.33±0.15 (1.30)	-
7 (n=9)	1.39±0.07 (1.39)	1.70±0.24 (1.75)	1.80±0.33 (1.75)	1.87±0.40 (1.74)	2.00±0.52 (1.88)	1.78±0.42 (1.73)	1.52±0.26 (1.60)

TABLE 5: Comparison of relative lengths of vertebral scutes among specimens bearing five, six, and seven vertebral scutes. Mean relative lengths compared with one-way ANOVA followed by Tukey-Kramer (q). Median relative lengths compared with Kruskal-Wallis test (KW) followed by Dunn's (mean rank difference = MRD) when parametric assumptions violated. Pairwise comparisons made between specimens bearing five and six vertebrals (5 vs. 6) and those with five and seven vertebrals (5 vs. 7). a = 0.05 in all cases.

Scute	Variation Significant?	Test Statistic & P value	5 vs. 6 Verts	5 vs. 7 Verts
Vert1	no	F=0.07 P=0.93	n/a	n/a
Vert2	yes	KW=13.16 P<0.01	MRD=43.87 P<0.05	MRD=67.97 P<0.001
Vert3	yes	F=15.55 P<0.0001	q=4.65 P<0.01	q=7.48 P<0.001
Vert4	yes	KW= 16.39 P<0.001	MRD=51.9 P<0.01	MRD=76.2 P<0.001
Last Vertebral	yes	F=9.04 P<0.001	q=4.44 P<0.01	q=5.97 P<0.001

1956, 1958; Mosimann and Bider, 1960; Stickel and Bunck, 1989; Ernst et al., 1998).

Notochelys platynota is unique in normally having more than five vertebral scutes (Ernst and Barbour, 1989; Ernst et al., 2000). Six and seven vertebrals are the most commonly observed numbers. Of 127 specimens examined, 3.9% (n = 5) had five vertebrals, 85.0% (n = 108) had six vertebrals, 10.2% (n = 13) had seven vertebrals, and 0.8% (n = 1) had eight vertebrals (Fig.4). Two specimens with eight and five vertebrals, respectively, had noticeable abnormalities in the vertebral series. The specimen bearing eight vertebrals was severely deformed. The extra scutes were not aligned with the normal ones and had no definite position in the series. These deformed specimens were not used in the statistical analyses that follow.

In specimens with five vertebral scutes (presumably the ancestral condition), all scutes were large (Table 3) and broader than long (Table 4). All vertebrals were of similar length (KW = 6.47, P > 0.10; Table 3) and Vert4 and 5 were the narrowest (Table 4). In specimens with six or seven vertebrals, the first four and last (Vert6 or 7) vertebrals were large (Table 3) and broader than long (Table 4). Those vertebrals between the fourth and last (Vert5 or Vert5-6), however, were smaller (Table 3) and occasionally longer than broad (5% of specimens, n = 5).

Vert5 was shortest in specimens (95%, n = 91) with six vertebrals (Table 3). A few specimens (5%, n = 5) had Vert4 or 6 as the shortest. In most of these cases (n = 4), however, Vert5 was still the narrowest. Variation among the median relative lengths of all vertebrals was significantly greater than expected by chance (KW = 381.63, P < 0.0001). Vert5 had the smallest median relative length (11.3%) and was significantly different from the median relative lengths of all other vertebrals (Dunn's, P < 0.001 in all cases).

Verts5 and 6 were shortest (67%, n = 6) when seven vertebrals were present (Table 3). A few specimens (33%, n = 3) had Verts4 and 6 as the shortest. Variation among the mean relative lengths of all vertebrals was significantly greater than expected by chance (F = 30.06, df = 62, P < 0.0001). Verts5 and 6 had the smallest mean relative lengths (Table 3) and were significantly different from the mean relative lengths of all other vertebrals (Tukey-Kramer, P < 0.001 in all cases except Vert4 vs. Vert5, P < 0.05 and Vert4 vs. Vert6, P < 0.01). These shorter scutes represent the extra vertebrals characteristic of this species.

Variation among the median relative lengths of the entire vertebral series for specimens with five (median = 99%), six (median = 96%), and seven (median = 93%) vertebral scutes was not significantly greater than expected by chance (KW = 2.08, P = 0.35). This suggests that the presence of supernumerary scutes does not result in an increase in the relative length of the vertebral series (i.e. at the expense of the marginals/cervical/supracaudals). Instead, as we shall see below, there is a shortening of some scutes to accommodate the additional ones.

Variation among the mean or median width to length ratios of Vert2 (F = 3.16, df = 106, P < 0.05), Vert4 (KW = 12.52, P < 0.01), and the last vertebral (F = 7.39, df = 107, P < 0.01) in specimens with five, six, and seven vertebral scutes was significantly greater than expected by chance (Table 4). The median width to length ratios for Vert4 were significantly different between specimens with five and six vertebrals (MRD = -49.22, P < 0.01) and between those with five and seven vertebrals (MRD = -65.53, P < 0.01). The mean width to length ratios for Vert2 (q = 3.5, P < 0.05) and the last vertebral (q = 4.84, P < 0.01), however, were significantly different between specimens with five and seven vertebrals only (Table 4). In all of the above comparisons, specimens with five vertebral scutes had the smallest mean or median length to width ratios. As we shall see below, the increase in the width to length ratios of the normal vertebral scutes in specimens with six or seven vertebrals is due primarily to decreases in their lengths.

In specimens with six or seven vertebral scutes, the widths of all normal vertebrals were seemingly unaffected by the presence of the extra vertebral scutes. With the exception of Vert1, however, their lengths were noticeably shorter than in specimens with five vertebral scutes (Tables 3 and 5), presumably to accommodate the extra scutes. The fourth and last (Vert6 or 7) vertebrals were particularly affected, as these were the shortest of the normal vertebrals in the series (Table 3).

Variation among the mean or median relative lengths of Vert2-4 and the last vertebral in specimens with five, six, and seven vertebrals was significantly greater than expected by chance (Table 5). The mean or median relative lengths of Vert2-4 and the last vertebral were significantly different between specimens with five and six vertebrals (Table 5) and between those with five and seven vertebrals (Table 5). In all comparisons, specimens with five vertebrals had the greatest mean or median relative length.

Based on these evidences, it seems possible that the extra vertebrals in *Notochelys* originated through symmetrical subdivisions of the fourth and last (Vert6 or 7) vertebral scutes along with the shortening of the second and third. However, as suggested by Cherepanov (1989), the extra vertebrals may not be due to subdivisions of existing scutes but rather a result of the *de novo* appearance of supernumerary vertebral placodes (growth nodes) during the early stages of embryological development. In either case, the scute proportions reported above indicate a specific packing arrangement to accommodate an extra number of growth nodes (P.P. van Dijk, pers. comm.).

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