

# Function of Complexly Fluted Septa in Ammonoid Shells

## II. Septal Evolution and Conclusions

By

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With 8 figures and 3 tables in the text

HEWITT, R. A. & WESTERMANN, G. E. G. (1987): Function of complexly fluted septa in ammonoid shells. II. Septal evolution and conclusions. – N. Jb. Geol. Paläont. Abh. 174: 135–169; Stuttgart.

**Abstract:** The depressed and fluted septal morphology of the early whorls of typical Ammonoidea, with a spherical ammonitella, had a circumferential support function in an offshore breeding organisms adapted, for r-mode selection strategy. Later ontogenetic stages of most Phylloceratina and some other taxa continued the circumferential support function of septal fluting. Other ammonoids can be regarded as having septa developed into an anticlastic cylinder morphology, which was largely adapted to resist hydrostatic pressures applied via the body and shows significant correlations between the number of umbilical flutes and whorl shape.

**Zusammenfassung:** Die flachen, gefalteten Septen in den Innenwindungen typischer Ammonoideen, mit sphärischer Ammonitella, funktionierten als Abstützung gegen den zentripetalen Außendruck in Organismen, welche einem Selektionsdruck vom r-Typus unterlagen. Diese Stützfunktion blieb bei den meisten Phylloceratina und einigen anderen Taxa auch in späteren ontogenetischen Stadien erhalten. Die Septen anderer Ammonoidea können als antiklastische Zylinderformen angesehen werden, die so gebaut waren, daß sie dem hydrostatischen Druck des Weichkörpers widerstanden. Die Zahl der Umbilical-Loben korreliert signifikant mit dem Windungs-Querschnitt.

**Key words:** Ammonoids, shells, stresses, septa, sutures, Jurassic.

### 1. Introduction, method and terminology

In part I of this study HEWITT & WESTERMANN, (1986) briefly reviewed and discussed the mechanical principles involved in the statics of ammonoid shells. Two general models were proposed to explain the function of phragmocones. In the 'Pfaff model' the critical stresses in the septa result from

an hydrostatic load applied to the last septum via the body chamber. In the 'Westermann model' the septa have also an internal support role which extends the implosion depth of the shell wall.

### 1.1 Theoretical structural parameters

The structural principles were used to define a number of theoretical parameters and constants illustrating the maximum-stress theory of ammonoid implosion. The siphuncle strength index (WESTERMANN 1971, revised 1982) only implies approximate depth limits. The experimental work of CHAMBERLAIN & MOORE (1982) implies that the thicker connecting rings of the early whorls of ammonoids and *Nautilus* may have had half the tensile strength of freshly grown adult rings. The remeasured decrease of the siphuncle strength index during the whole ontogeny of *Nautilus pompilius* is equivalent to range of tensile strength from about 45 to 77 MPa (index 11 to 18) and results from variation in the horny tube of juvenile growth stages. *Nautilus pompilius* specimens killed at a phragmocone diameter of 50 mm have a siphuncle strength index of 11 to 17 throughout ontogeny, like the later stages of mature specimens with an equivalent diameter of 110 mm. The great depth estimated from inner whorls of *Goniatites* and *Stephanoceras* may or may not be an overestimate.

- B = Index of shell wall bending strength (resulting from sutural support, not  $R_1$  and  $R_2$ ) relative to the *Nautilus* lateral lobe =  $10.3^2/(l/d_w)^2$  (section 1.2.).
- C = Index of circumferential strength of the marginal septum (again relative to *Nautilus*) =  $10.3/(L/Y \cdot d_s)$ .
- $\Delta$  = Septal spacing.
- $d_w$  = Thickness of shell wall (minimum within  $R_1$  and  $R_2$ ) measured with a scale typically composed of c. 22  $\mu\text{m}$  increments. In the error calculation it was assumed that 95% of the estimated values were within two increments of the correct mean value:  $1\sigma \sim (l/d_w \text{ as increments})/4$ .
- $d_h$  = Thickness of connecting ring in adult whorl. The error was defined in the same way as  $d_w$ , although the scale increments were generally reduced in size (c. 10  $\mu\text{m}$ ). The siphuncle strength index is =  $100 d_h/R_2$ .
- $d_c$  = Maximum septum thickness in the middle part of the chamber near the median plane of the shell. Error defined as in  $d_w$ .
- $d_s$  = Thickness of septa (average minimum)
- ISC = Index of sutural complexity (WARD 1980)  
= Suture length (Y)/Whorl circumference (X).
- K = cross-sectional area of whorl.
- l = Length of largest unsupported square of shell wall.
- L = Area of whorl potentially supported by a single septum.
- m = Weibull modulus (proportional to homogeneous distribution of large flaws in isotropic shells). (FELBECK & ATKINS 1984).  
=  $1.27 S_w/0.5 2\sigma \sim = 244 \text{ MPa}/20 \text{ MPa} = 12.32$
- O = Whorl overlap shape =  $100 W_h/0.5 W_b$ .
- P = Hydrostatic pressure deduced from shell strength in MPa. KANIE & HATTORI (1983) report that mature live *Nautilus pompilius* implodes at 7.89, 8.31 and 8.34 MPa pressure.
- $P_f$  = Probability of implosion due to tensile fracture.
- R = Internal radius of curvature measured with concentric rings on a transparent plastic sheet. Error taken as  $\pm 2 \sigma \sim = \pm 4\%$ , or defined by diameter measurement error.

- $R_1$  = Maximum inner radius. Variance  $R_1 = \text{variance } R_2 \cdot (R_1/R_2)$  unless  $\alpha$ .  
 $R_2$  = Minimum inner radius. Error  $R_2$  as  $R$ .  
 $r$  = Correlation coefficient (tested for significance at the 5% probability level using a t-test).  
 $S_c$  = Ultimate compressive strength of short columns of the *Nautilus* shell wall. The wide variation in these results is due to crushing and shearing in the experiments. It represents the maximum strength.  
 = 411 MPa  $\pm$  54.8 MPa  $2\sigma$  (based on 10 tests by CURREY 1976 and personal communication 1982).  
 $S_{cs}$  = Ultimate tensile strength in 29 nacreous surfaces of the *Nautilus* shell wall determined by the Modulus of Rupture (CURREY & TAYLOR 1974, CURREY 1976, CURREY personal communication 1982 and new data with about 30 mm<sup>3</sup> in tension).  
 = 193.0 MPa  $\pm$  10.65 MPa  $2\sigma$  when the standard error of the mean is used to estimate the strength variation in the shell (measured  $2\sigma = 40$  MPa).  
 $S_{cw}$  = Ultimate tensile strength in the outer prismatic layer of the shell wall determined by the ratio 182.5/109.0 MPa representing the maximum stresses of the outer and inner shell wall surface in tensile bending tests (CURREY personal communication 1982). The appropriate differential between the implied strength of the nacreous layer (184 MPa) and the mean cited above.  
 = 114.4 MPa  $\pm$  6.3 MPa  $2\sigma$ .  
 $S_{ch}$  = Ultimate tensile strength of the  $\alpha$ -chitin and protein connecting ring (LOWENSTAM et al. 1984) implied by the tests on *Nautilus* siphuncle A of CHAMBERLAIN & MOORE (1982). For various reasons the maximum stress implied by chamber 30 is the most appropriate strength. An illustrative error of  $S_{ch} \pm 4$  MPa  $2\sigma$  was incorporated into pressure estimates based on these siphuncles.  
 = 76.84 MPa  $\pm$  4 MPa  $2\sigma$ .  
 $S_{cn}$  = Tensile stress of nacre with a cumulative probability of fracture of 0.633 in bending tests = 200 MPa.  
 $S_t$  = Maximum working tensile stress required in adult life = 100 MPa.  
 $\pm 2\sigma$  Approximate 95% range of estimates, not excluding the possibility that the remaining 5% of estimates lie on one side of the mean. The  $2\sigma$  error of the pressure estimates is simply the mean multiplied by double the square root of  $(1\sigma \sim S/S)^2 + (1\sigma \sim d/d)^2 + (1\sigma \sim R_2/R_2)^2 + (1\sigma \sim R_1/R_1)^2$  when they are independent variables of equal weight. Real probabilities of implosion in nacre are predicted from the Weibull distribution function (FELBECK & ATKINS 1984):  
 $P_f = 1 - \exp[-(S_t/S_{cn})^m \cdot V]$  for volume change  
 $P_f = 0.50 = 193 \text{ MPa} / [2(m+1)]^{1/m} = 148 \text{ MPa}$  for c. 30 mm<sup>3</sup> in tension.  
 $U$  = Number of umbilical flutes (on one half of the septum). Defined as any saddle or foliole on the external suture with an amplitude  $\geq 10\%$  of that of the external saddle and lobe. Excludes external saddle and lateral saddle.  
 $V$  = Volume in tension/volume of c.30 mm<sup>3</sup> tested.  
 $Wb$  = Whorl breadth.  
 $Wh$  = Whorl height.  
 $Wh_v$  = Internal whorl height at venter.

## 1.2. Precision of theoretical implosion pressures

The problem of calculating the errors in the hydrostatic pressure estimates, was clarified by rewriting equations for membrane stress "S" in cylinders (e. g. connecting rings), hemispheres (e. g. nautiloid septa) and other synclastic surfaces of revolution (with  $R_2/d > 10$  and  $< \infty$  after Roark 1954).

$$\begin{aligned}
 P &= (S/2)/(R_2d) &= S/0.5 \cdot (R_2d/d) = S/(R_2/2d) &\text{Hemisphere} \\
 P &= S/1/(R_2d) &= S/1 \cdot (R_2/d) &\text{Cylinder} \\
 P &= 2(S/R_2/R_1)(R_2/2d) &&\text{Intermediate surface, e. g. whorls}
 \end{aligned}$$

In most cases the variances were added as proportions of the mean. Estimates from synclastic umbilicus arcs involve the variances of  $R_2$ ,  $d_w$  and  $S_w$ . The calculation of crushing pressures requires addition of the variances of  $R_1$ ,  $R_2$ ,  $d_w$  and  $S_c$ . Even in this case the accuracy of the mean as a stress estimate is typically only  $\pm 6\%$  (20~).

Despite the theoretical uncertainty about the stresses in anticlastic membranes, it is useful to calculate a strength index approximating to the anticlastic cylinder model of the ammonoid septum. In compressed whorls (e. g. *Placenticeras*) the axis of the cylinder is parallel with the median plane of the shell and the largest  $R_2$  radius (the smaller radius) approximates to 0.5 Wb. There are potential errors due to the development of an anticlastic hemisphere morphology in some *Phylloceras* (e. g.  $R_1 \cong R_2$  at  $d_w$ ) and occurrences of a larger radius of curvature in some whorls with  $R_1 > 0.5$  Wb. In depressed whorls and evolute taxa, the mid-line of cylindrical anticlastic symmetry curves round parallel to the surfaces of the whorls and the radius  $R_2$  is approximately equal to 0.5  $Wh_i$ .  $P_c = 193 \text{ MPa} \pm 2.7\% \text{ } 10\sim$  ( $\geq 0.5 Wh_i \pm \geq 2\% \text{ } 10\sim /d_w \pm \leq 4\% \text{ } 10\sim$ )

$$S \quad R_2 \quad d \quad R_1$$

Variance = 0.0007 +  $>0.0004$  +  $>0.00016$  +  $<0.0002$  =  $>0.0030$   
 Mean  $P_c$  (10 depressed taxa Fig. 8) =  $8.64 \text{ MPa} \pm 0.94 \text{ MPa } 20\sim$   
 Mean  $P_h$  from their siphuncle data =  $8.41 \text{ MPa}$  so  $S_{th} = 78.9 \text{ MPa} ?$

A sample of 17 depressed and compressed adult taxa showed a generally good linear correlation between this speculative pressure estimate  $P_c$  and that provided by the siphuncle strength index  $P_h$  (Fig. 8). If their septa failed at 193 MPa in the manner suggested above, then the mean ratio  $P_h/P_c$  implies that their connecting rings had a tensile strength of 74.15 MPa. Division of the naere strength by a factor of 1.5 suggested by juvenile *Nautilus* implosion data implies a mean phosphatic connecting ring strength of about 50 MPa. A similar analysis of the phosphatic horny tube of the nautiloid *Bactoceras* (HEWITT & STAIT 1985) yielded a tensile strength of 40 MPa.

The statically indeterminate problem posed by the support functions of the septa in weak parts of the shell wall, are illustrated by the lateral lobe of the fourth septum behind the *Nautilus* body chamber. The local crushing pressure of  $9.6 \pm 1.8 \text{ MPa}$  (20~) is implied by  $P_c = S_c/(2-R_2/R_1) \cdot (R_2/2d_w) = 411 \text{ MPa}/(2-65/230 \text{ mm}) \cdot (65 \text{ mm}/2.62 \text{ mm})$ . The weakest part of the shell wall is the outer layer overlying the axial plane of the cylindrical pillar-flute of the lateral lobe. In this region the suture is aligned parallel to the hoop stress of the shell wall and would generate an internal compressive stress proportional to  $\Delta/d$ , ( $= 12.0 \text{ mm}/0.9 \text{ mm}$ ) and the circumferential strength index  $C$  of ammonoid sutures. If the shell wall was flat and simply supported on the sutures, then the outer shell wall would break at 7.8 MPa hydrostatic pressure and produce an 104 MPa compressive stress along the pillar-flute ( $P_t = S_w/0.2214$  ( $l = 10.68 \text{ mm}/d_w = 1.31 \text{ mm}$ )<sup>2</sup>). An index of  $B = 1.0$  represents a critical pressure of 4.8 MPa on a flat sheet of tensile strength  $S_{tw}$ . Strain gauges imply that this bending stress model is more appropriate than the membrane stress model.

### 1.3 Conversion to probable depth limits

The Modulus of Rupture is defined as "the fictitious tensile or compressive stress in the extreme fibre of a beam computed by the flexure equation" (ROARK 1954), and is only strictly applicable to the implosion of the shell wall

by bending over the septal sutures with minimal plastic strain (HEWITT & WESTERMANN 1986, Fig. 6). CURREY & TAYLOR (1974) imply that the Modulus of Rupture is a three-fold overestimate of the measured tensile strength of nacre in pure uniaxial tension; a consequence of the increased frequency of Griffith flaws in large volumes of shell, the plastic deformation of samples in bending and damaged samples. It merely sets limits to the imagination of sceptics who doubt the calibration of ammonoid shell strength based on *Nautilus* implosion data (e. g. CHAMBERLAIN & MOORE 1982, 416).

The real implosion pressures and implied depth limits of ammonoids are not specifically described in this paper. It is emphasised that the constants given above are maximum values which need to be scaled down by appropriate safety factors. These safety factors are divisible into biological safety factors defined by habitat and observed implosion depths (typically 1.3 or more in *Nautilus*, see KANIE & HATTORI 1983), time-related safety factors appropriate for connecting ring and dried nacre (less than 2.2), and an instantaneous safety factor of 1.5 for large volumes of *Nautilus* nacre in tensile plane stress. The cited pressures for the tensile implosion of nacre can be divided by  $1.5 \times 1.3$ , prior to multiplication by a factor of about 100 to give the equivalent approximate habitat depth limit in metres.

## 2. Functional aspects of sutural evolution

### 2.1 Ancestral goniatitic sutures

The increase in sutural complexity from orthoconic *Bactrites* to involute *Goniatites* was probably related to a circumferential support function within the compressed subrectangular whorls of the Middle Devonian goniatites. The lobes of *Bactrites* merely reflect the marginal position of the septal necks (Table 1, based on WIEDMANN 1966, Fig. 37). But it would be incorrect to regard typical goniatites as having a weaker phragmocone wall than their bactritid ancestors. This is illustrated by a comparison of *Goniatites* (*Dombartites*) *choctawensis* (CM 176) and *Bactrites quadrilineatus* GIRTY (CM 177) from the same Lower Carboniferous locality.

The hemispherical septa of *Bactrites* would have broken by tensile membrane stresses at a maximum pressure of  $6.94 \pm 0.64$  MPa ( $2\sigma$ ). The connecting ring would have ruptured at a pressure of less than  $13.1 \pm 2.0$  MPa ( $2\sigma$ ) and the unsupported cylindrical shell wall would have been crushed by compressive membrane stresses at a maximum pressure of  $17.30 \pm 2.4$  MPa ( $2\sigma$ ). It would probably have been broken by axial bending stresses, and according to the model of BROWNELL & YOUNG (1959: 144) it would have buckled at 1.0 MPa without septal sutures and at 40 MPa with sutures ( $\Delta/R_2 = 0.7$ ).

Any risk of failure due to buckling was greatly reduced by coiling in *Goniatites*. The connecting ring in a 20 mm diameter whorl implies a rupture depth of less than  $10.5 \pm 0.64$  MPa ( $2\sigma$ ). The unsupported shell wall would have been crushed at a pressure of  $12.0 \pm 1.87$  MPa ( $2\sigma$ ) and resembles a hemispherical surface buckling at about the same or slightly higher pressure (e.g. Brownell & Young 1959: 151). The inner tensile arcs around the narrow umbilicus (Fig. 1) would have broken at a pressure  $17.75 \pm$

Table 1. Structural parameters for representative ammonoids, based on specimens at McMaster University and cited literature.

	X√K.	O	U	Dia. mm	R <sub>1</sub> mm	R <sub>2</sub> mm	d <sub>w</sub> μm	d <sub>i</sub> μm	ISC	B	C
<i>Bacrites</i>	3,55	0	0		∞	7.65	322		1.09	0.38	0.63
<i>Goniatites</i>		82	0	21	15	8.5	78	120	1.79	0.85	0.52
<i>Schistoceras</i>		60	2						3.24		
<i>Schumardites</i>		78	3	57	72	51	444	330		1.67	1.38
<i>Properrinites</i>		85	4	65	60	33	267	110			
<i>Perrinites</i>		103	5.5	50		34					
<i>Hyattoceras</i>		160	11						4.85		
<i>Trachyceras</i>		67	2.5								
<i>Joannites</i>		172	25								
<i>Arcestes</i>		95	13	35	55	17.6	356	25		0.67	29.7
<i>Pinacoceras</i>		320	23								
<i>Parapinacoceras</i>		175	13								
<i>Discoceratites</i>			3						1.80		
<i>Stenopopanoceras</i>		81	7.5								
<i>Megahyllites a</i>		45	3								
<i>Megaphyllites b</i>		39	6.5								
<i>Sowerbyoceras</i>		54	3.5								
<i>Phylloceras a</i>		130	6	80	300	68.4	600			7.9	
<i>Phylloceras b</i>		116	7	30					10.15		
<i>Phylloceras c</i>				30					10.84		
<i>Phylloceras d</i>		140	7	63							
<i>Euphylloceras</i>			9						7.19		
<i>Hypophylloceras</i>			5						3.93		
<i>Calliphylloceras a</i>				110					<14.29		
<i>Calliphylloceras b</i>		150	>9	100	∞	67.6	511			13.4	
<i>Calliphylloceras c</i>										11.8	11.9

	X√K.	O	U	Dia. mm	R <sub>1</sub> mm	R <sub>2</sub> mm	d <sub>w</sub> μm	d <sub>v</sub> μm	ISC	B	C
<i>Calliphylloceras</i> d		182	6	52							
<i>Tragophylloceras</i>	5.35			17					3.58		
<i>Ectocentriles</i>									11.65		
<i>Eurysomites</i>									4.85		
<i>Trachyphyllites</i>		12	3						6.30		
<i>Lytoceras</i> a	3.6	3	1	130	∞	22.5	1620				
<i>Lytoceras</i> b			9	200					34.61		
<i>Gaudryceras</i> a									15.56		
<i>Gaudryceras</i> b		7.5				15			9.43		
<i>Protetragonites</i>									7.42		
<i>Tetragonites</i> a	4.49		8			30.0			5.08		
<i>Tetragonites</i> b	3.78		3.5			1.7			5.09		
<i>Tetragonites</i> c			3.5						4.73		
<i>Kosmatella</i>	3.90		5			3.6			5.94		
<i>Jauberticeras</i>	4.53		5			15.5			6.39		
<i>Hoploscaphites</i> a			2.5			8			3.52		
<i>Hoploscaphites</i> b		54		38	5	3.9*	220	60		1.3	
<i>Hoploscaphites</i> c		53		24	∞	8.7	177				
<i>Hypoturritiles</i>		0							6.65		
<i>Didymoceras</i> a		0		100	100	18	1340				
<i>Didymoceras</i> b		0		100	18*	17*	1340				
<i>Turritiles</i> c		0							10.28		
<i>Pseudhelicoceras</i>		0							20.48		
<i>Hyphantoceras</i>		0							14.80		
<i>Neocrioceras</i>		0							11.96		
<i>Diplomoceras</i>		0							16.38		
<i>Pravitoceras</i>		0							13.49		
<i>Baculites</i> a		0			∞	25	1420				

	X√K.	O	U	Dia. mm	R <sub>1</sub> mm	R <sub>2</sub> mm	d <sub>a</sub> μm	d <sub>i</sub> μm	ISC	B	C
<i>Baculites</i> b		0			∞	160	3000				
<i>Baculites</i> c		0			16	30 <sup>*</sup>	3000				
<i>Psiloceras</i>				60	∞	16.4	300				
<i>Asteroceras</i>				35	∞	11	400	60		1.7	
<i>Radstockiceras</i>	6.94	305	5.5	30					6.01		
<i>Oxynoticeras</i>		340	1.5	40							
<i>Echioceras</i> a = vent./lat.		10	2	110	14 <sup>*</sup>	3	645				
<i>Echioceras</i> b = vent.		10	2	110	70	25	645				
<i>Echioceras</i> c = lat.		10	2	110	23	11 <sup>°</sup>	645	100		1.06	
<i>Echioceras</i> d = lat.		10	2	110	∞	23	645	100		1.06	
<i>Dactylioceras</i> a	4.09	39	1	75		9.6			2.817		
<i>Dactylioceras</i> b lat.		35		60	∞	16	335				
<i>Dactylioceras</i> c lat.		25		75	∞	17.0	350	70			
<i>Liparoceras</i> a vent.				40	22	12.0	445				
<i>Liparoceras</i> b lat.		69	2	90	∞	27.5	490				
<i>Phlysegrammoceras</i> a lat.		150	8	150	∞	90	2400	275		30	
<i>Hildoceras</i> a lat.				115	∞	22	1550	180		5.2	
<i>Dorsetensia</i>	5.26	150									
<i>Ludwigia</i> a		130		95	∞	50	1100		5.2		
<i>Ludwigia</i> b		130		95	∞	65 <sup>c</sup>	1100	130		14.2	
<i>Ludwigia</i> c		187	7.5	162							
<i>Graphoceras</i>				80	∞	62 <sup>c</sup>	1000				
<i>Hammatoceras</i>		58	4.5	270							
<i>Sonninia</i> a		81	8	80							
<i>Sonninia</i> b				70	∞	35	450	70		4.7	
<i>Stephanoceras</i> a vent. lat.		26	2.5	30	19	10.2	265	40			
<i>Stephanoceras</i> b vent. lat.		26	2.5	70							
<i>Stephanoceras</i> c vent. lat.		24	2.2	30	25	12.6	420				

	X√K.	O	U	Dia. mm	R <sub>1</sub> mm	R <sub>2</sub> mm	d <sub>w</sub> μm	d <sub>l</sub> μm	ISC	B	C
<i>Stephanoceras</i> d vent. lat.	4.04	29	8	108					15.45		
<i>Stephanoceras</i> e vent. lat.	4.23	24	4	35&44					8.32		
<i>Zemistephanus</i>			3	54					11.91		
<i>Zemistephanus</i>	3.98	25	4.5	34					11.97		
<i>Sphaeroceras</i>	4.84	56	3	16&20					4.51		
<i>Chondroceras</i> a	4.94	70	8	32					4.92		
<i>Chondroceras</i> b		77	7	29					9.79		
<i>Chondroceras</i> c			7	11					5.80		
<i>Eurycephalites</i>				64					7.63		
<i>Xenocephalites</i>				30					4.86		
<i>Macrocephalites</i> a			5.5	38					9.24		
<i>Macrocephalites</i> b			4.5	70					7.63		
<i>Macrocephalites</i> c			6	132					9.13		
<i>Macrocephalites</i> d lat.				60	∞	47.5	620	70			
<i>Macrocephalites</i> e lat.		96		125	∞	95	1600	155			
<i>Macrocephalites</i> f lat.		116	9	145	150	63	1110		34.61	15	
<i>Macrocephalites</i> g umbil.		116		145	∞	7.5*	580				
<i>Epimayaites</i> a			5	83					11.73		
<i>Epimayaites</i> b			11	125					12.38		
<i>Emileia</i> a vent.		125		50	30	20	425	100		5	
<i>Emileia</i> b umbil.			125	50	5	2.5	600				
<i>Collotia</i> a	4.14	50		8.5	180				25.61		
<i>Collotia</i> b	4.07	55		5.5	140				13.31		
<i>Collotia</i> c	3.84	25		5.5	130				20.93		
<i>Collotia</i> d	4.15	50		6.5					12.17		
<i>Collotia</i> e	3.86	25		4.5	60				11.26		
<i>Olcostephanus</i> a	4.49				10				3.53		
<i>Olcostephanus</i> b	4.45	45		4.5	36				6.82		



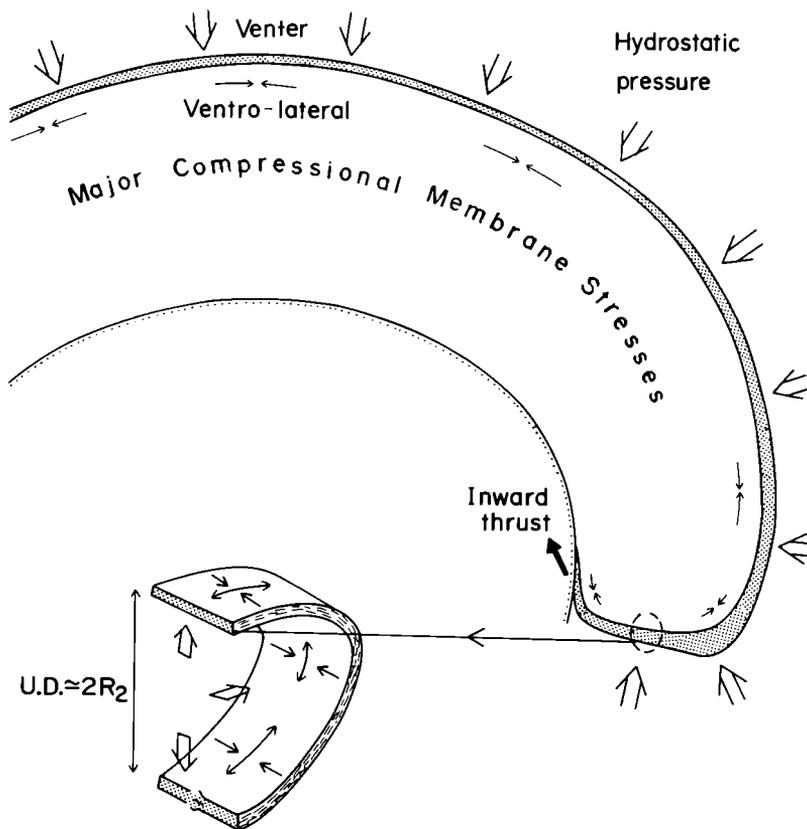


Fig. 1. Diagrammatic transverse section of a whorl of *Goniatites choctawensis* (CM 176). Note the variation in compressive membrane stress related to the transverse curvature radius and shell thickness, in addition to the tensile axial stresses generated by the large umbilicus diameter (U.D.). The inner whorls of the same specimen are seen in the more tangential section shown on Fig. 2.

1.0 MPa ( $2\sigma^-$ ). Thus the increased strength indices of the *Goniatites* sutures (HEWITT & WESTERMANN, 1986, Fig. 5 A-B; Fig. 2, Table 1) and the greater potential support role of the septa, did not actually influence implosion depth.

Since the fluted septa and flattened wall surfaces of *Rectoclymenia* (number of umbilical flutes  $U = 0$ , whorl overlap shape  $O = 75$ ) and *Sphenoclymenia*

( $U = 1.5$ ,  $O = 64$ ), were liable to have been broken by bending stresses, it is only to be expected that the larger *Sphenoclymenia* would have evolved a more complex suture. Thus the argument of SCHINDEWOLF (1972: 50) does not weaken the case for a functional control of goniatitic suture morphology. The potential decrease in wall strength, made possible by the removal of axial bending stresses within involute shells, required an increase in the critical Euler stress of the last septum. Further reductions in wall strength were permitted by the increased support function of internal septa and resulted in the evolution of more streamlined phragmocones.

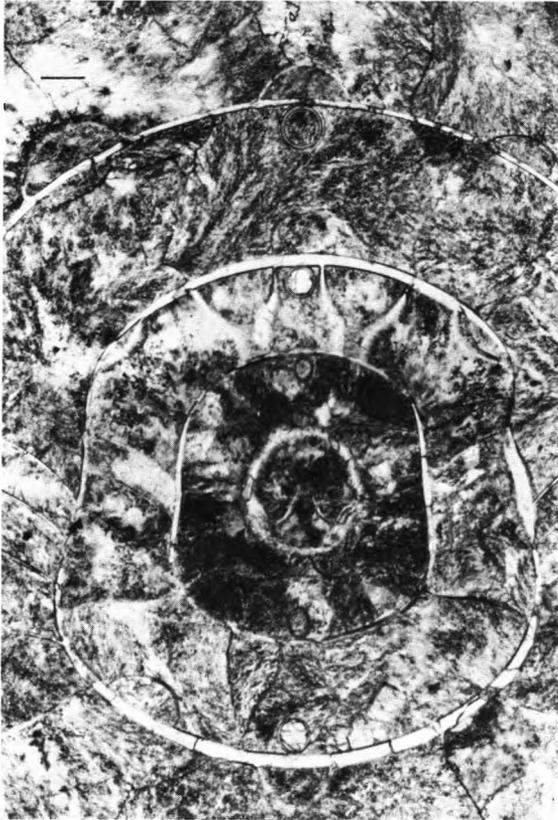


Fig. 2. Slightly tangential transverse section of the inner whorls of *Goniatites choctawensis* (CM 176), showing the unusually thick shell wall and phosphatic connecting ring. Also note the sinuous goniatitic suture cut tangentially in the first whorl (Bar scale = 0.2 mm,  $\times 43$ ).

## 2.2 Schumarditaceae

Lower Permian Schumarditaceae had ammonitic sutures which anticipated both the density and the form of complex Mesozoic sutures. They attained a shell diameter of 300 mm and had a global range. They died out before the Permo-Triassic extinction. Their sutural 'design' reappeared after an interval of some 30 Ma, in Anisian *Parapinacoceras* and persisted in the Phylloceratina until the final extinction of the ammonoids.

The ancestral goniatitic sutures were studied in a *Schumardites* (CP28) with a similar size and shape to the ammonitic *Perrinites* illustrated by MILLER et al. (1957; fig. 60). Their implosion depths are as yet unknown. The flanks of *Schumardites* phragmocones had a greater radius of curvature than those of *Perrinites* ( $R_2 = 51$  versus 34 mm) and would have been crushed at a pressure of  $5.54 \pm 0.80$  MPa ( $2\sigma$ ) without support. The unsupported last whorl of the phylogenetically intermediate *Properrinites* (Table 1) may have been crushed at a pressure of  $4.58 \pm 0.68$  MPa ( $2\sigma$ ). The smaller length of the largest unsupported square ( $l$ ) on *Perrinites* (0.6 vs. 3.5 mm in *Schumardites*) presumably permitted a reduction in shell thickness.

## 2.3 Cyclolobaceae

The middle and Upper Permian Cyclolobidae and Hyattoceratidae evolved ammonitic sutures from a multi-lobed ceratitic lineage of the Goniatitina (Marathonitaceae, see CHAO 1980). They were characterised by overlapping whorls and a rapid increase in U (number of umbilical flutes) with O (Fig. 3, whorl overlap shape). A 100 mm diameter *Cyclolobus* shows 13.5 U at 207 O; *Timorites* shows 11 U at 96 O and 8 U at 111 O; *Waagenoceras* shows 7 U at 79 O; and *Hyattoceras* shows 11 U at 160 O (MILLER et al. 1957, RUZHENTSEV 1976). The more complex phylloid sutures are widely spaced and display angles of up to  $45^\circ$  between the plane of the septum and the plane of the circumferential hoop stress. The curvature radius of the lateral shell wall was considerably greater than in similar sized *Perrinites*. The ventrally retracted, convex-out curvature of these septa reappeared in the similar shaped whorls of Middle Triassic *Joannites*.

## 2.4 Ancestral Ceratitic sutures

The ancestors of the Mesozoic Ammonoidea are represented by the Upper Carboniferous Medicottiaceae and the Lower Carboniferous Prolecanitida (WIEDMANN & KULLMANN 1981). Namurian representatives show sutural complexity evolving independently of the static, long-ranging "morphotype two" of SAUNDERS & SWAN (1984: 210). It is a smooth compressed shell, with a flattened or acute venter, found within shallow-water carbonate facies.

A correlation between the number of ceratitic saddle-flutes and the ontogenetic increase in whorl compression, has been described in Permian Medicottiidae (RUZHENTSEV 1946, SEILACHER 1975, CHERNOV 1961) Medicottiid siphuncles from acid-insoluble residues of the lower Riepetown

Formation (samples provided by Dr. R. H. MAPES), have strength indices (sensu Table 3) of 7.0 at an internal radius of 0.3 mm, indicative of rupture pressure of less than  $5.4 \pm 2.7$  MPa (2 $\sigma$ ).

The Triassic Ammonoidea evolved via a few small genera belonging to the Permo-Triassic Xenodiscaceae and Otocerataceae (SCHINDEWOLF 1954, KUMMEL 1969, TOZER 1981). Transverse ribbing was more common in these Mesozoic ceratitines than in goniatites. These superfamilies included the rectangular and overlapping whorls of *Discotoceras*, the subrectangular and compressed whorls of *Xenaspis* and the laterally concave whorls of *Prototoceras*; all of which probably required support from ribbing or sutures if they lived at moderate depth. The goniatitic and ceratitic sutures are some of the simplest known, with an ISC that was often less than that of their goniatitic Lower Carboniferous ancestor *Protocanites* (2.56, WARD 1980) or their ceratitic descendant *Discoceratites* (Table 1). There is no correlation between U (mean 0.9) and O (mean 80, range 28 to 134) in a sample of 10 genera from ARKELL et al. (1957).

The remaining Scythian (Lower Triassic) ammonoids descended from this root-stock display a wider range of sutural and whorl morphology, but only 2 out of a sample of 45 genera have ammonitic sutures (ARKELL et al. 1957). *Lanceolites* has 5.5 U at 188 O and *Usseria* has 3.5 U at 103 O. The highly compressed Hedenstromiidae contain up to 6.5 ceratitic umbilical flutes and the 45 genera show the following significant regression of U on O:

$$U = 0.023 O - 0.079 \quad (r = 0.749)$$

$$\text{Range of } O = 22 \text{ to } 229; \text{ range of } U = O \text{ to } 6.5$$

## 2.5 Middle and Upper Triassic sutures

Most Middle and Upper Triassic ammonoids show a similar relationship between U and O, despite increased sutural complexity. A sample of 19 genera with ammonitic sutures, which excluded the Megaphyllitaceae, Arcestaceae and Pinacocerataceae of TOZER (1981), showed the following significant regression of U on O:

$$U = 0.021 O + 0.614 \quad (r = 0.744)$$

$$\text{Range of } O = 13 \text{ to } 220; \text{ Range of } U = 0.5 \text{ to } 7.0$$

The simplicity of these ammonitic sutures contrasts with those of Triassic ammonoids showing a rapid increase in U with O. Although the parameter U probably overestimated the number of saddle-flutes in these complex sutures, there is little doubt that the more fluted and overlapping septa display the most complex sutures. The generally convex-out septal curvature of *Joannites* and *Pinacoceras* contrasts with the straight sutural-zones (between saddle envelopes) of their relatives *Arcestes* and *Parapinacoceras* (Table 1, see also ARKELL et al. 1957, VAVILOV 1978, ZAKHAROV 1977). TINTANT et al. (1982)

postulated that these Triassic "shallow-water septa groups" became extinct and were replaced by the Jurassic descendants of the "oceanic" Phylloceratida and Lytoceratina.

The globular and depressed morphology of the *Arcestes* whorls is so similar to *Goniatites*, that it is interesting to compare the mechanical characteristics. An *Arcestes* (TR13) shows a lateral shell wall (Table 1), that would have been crushed by membrane stress at a pressure of  $9.90 \pm 1.44$  MPa ( $2\sigma^-$ ), without support from 23 septa per whorl. There are 16 septa per whorl in *Goniatites*. The umbilical wall of *Arcestes* ( $d_w = 178 \mu\text{m}$ ) would have broken in tension at a pressure of  $11.5 \pm 1.0$  MPa ( $2\sigma^-$ ). The sutures had a bending strength index (B) of 35 times the index in *Goniatites* (Table 1). The five-fold reduction in marginal septum thickness could explain the increase in their complexity (ISC). But the symmetrical lobules and folioles of *Arcestes* are unlikely to have supported the shell wall.

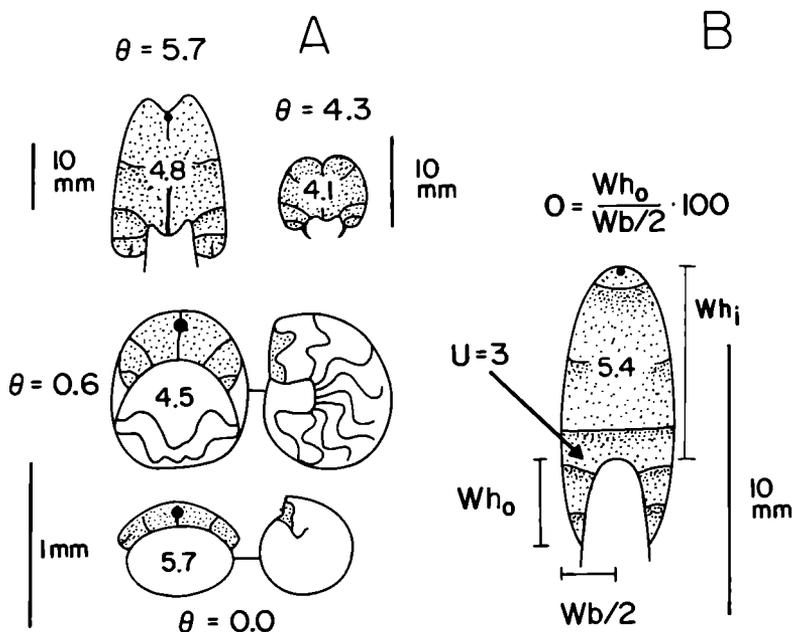


Fig. 3. Whorl sections showing variation in the dimensionless surface-to-volume ratio ( $X/\sqrt{K}$ ) and the whorl overlap shape  $O$ . A) *Euhoplites* based on MIKHAILOVA (1975) showing the proseptum ( $\Theta = 0$ ), a less depressed goniatitic septum from the first whorl ( $\Theta = 0.6$ ), a rounded adolescent whorl resembling those with the smallest surface-to-volume ratio ( $O = 4.3$ ), and a more sulcate, compressed adult whorl ( $\Theta = 5.7$ ).  $\Theta$  = number of whorls. B) *Tragophylloceras* based on SWINNERTON & TRUEMAN (1918) showing the overlap whorl height ( $Wh_i$ ) and half-whorl breadth ( $Wb$ ) parameters used to calculate  $O$ .  $U$  = number of umbilical flutes. Note that this compressed adult septum has a slightly smaller surface-to-volume ratio than the depressed proseptum of *Euhoplites*.

## 2.6 Phylloceratina

WIEDMANN & KULLMANN (1981) plausibly interpreted Triassic Ceratitina (*sensu* TOZER 1981) such as the Megaphyllitaceae, as being closely related to the Jurassic and Cretaceous Phylloceratina. They had multifluted septa showing ceratitic differentiation of the suture line and little relationship between U and O. Table 1 includes juvenile sutures of *Megaphyllites* (a) and *Sowerbyiceras* (WIEDMANN 1972, SCHLEGELMILCH 1976), mature sutures from a single *Stenopopanoceras* (VAVILOV 1978) and representative adult Phylloceratina (SCHINDEWOLF 1962, JOLY 1976, HALL & WESTERMANN 1980, SWINNERTON & TRUEMAN 1918).

The Jurassic Phylloceratidae provide evidence that ammonitic sutures were adapted to support the shell wall against hydrostatic pressure, without introducing major tensile bending stresses into the outer shell wall. A *Calliphylloceras* whorl (J1280) with a remeasured adult siphuncle strength index (18)

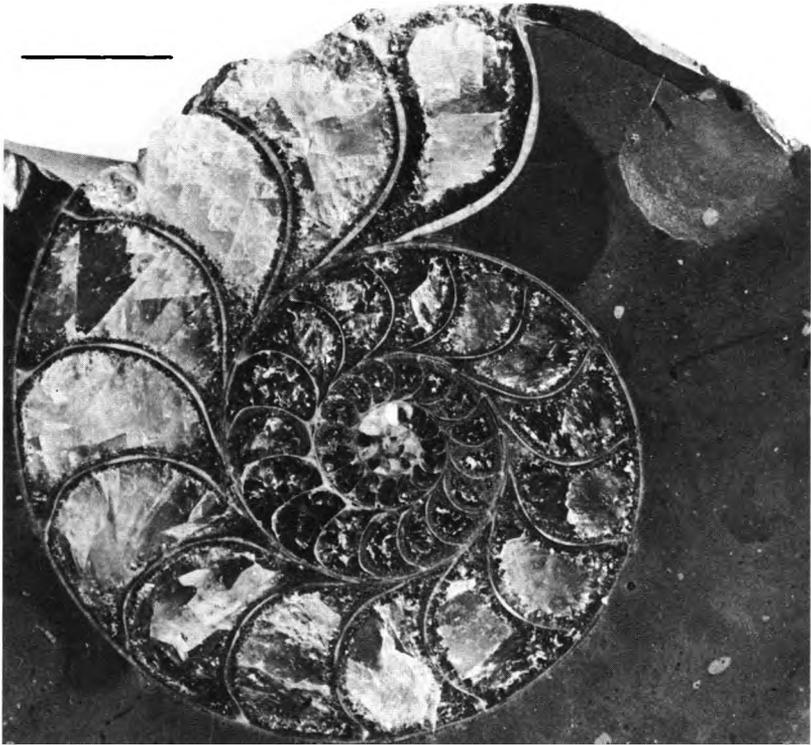


Fig. 4. Polished sagittal section of *Ptychophylloceras* (J2026g) showing the thickness of the (white) septa in the middle of the chambers and the extension of the connecting ring into the sediment-filled body chamber (bar scale = 10 mm).

indicative of an approximate rupture pressure of 14 MPa, would have been crushed at a pressure of  $3.11 \pm 0.46$  MPa ( $2\sigma$ ) without septal support (b on Table 1). A similar specimen (J1826, c on Table 1) has 12 times the sutural strength index of the *Nautilus* lateral lobe. Both the *Nautilus* and *Calliphylloceras* sutures were required to increase the wall crushing depth by a factor of two. This suggests that ammonoid saddle-flutes had more flexibility than pillar-flutes and were therefore less likely to rupture the outer shell wall by producing unwanted tensile stresses.

HENDERSON (1984) doubts the siphuncular evidence for a relatively deep-water habitat in the Phylloceratina (WESTERMANN 1971, 1982), despite the great thickness of the middle region of their septa in most genera (Figs. 4 and 8). Questionable use of the synclastic membrane stress formula, as an indication of the maximum strength of the septum centre in the Pfaff model, suggests that the anticlastically curved last septum of the analysed specimen J1280 may have broken in tension at a pressure of 40 MPa ( $d_s = 1.0$  mm at  $R_1 = R_2 = 10$  mm,  $\sigma = 193$  MPa). The implied four-fold safety factor could be taken as evidence that the thick septum was likely to break under an additional circumferential load. But if the habitat depth was much less than that required to break the unsupported shell wall (500 m), then the greatly reduced circumferential load implies a ten-fold decrease in strength merely due to anticlastic curvature. This apparent waste of shell material and buoyancy would be inconsistent with the more epipelagic habitat assumed by HENDERSON (1984). The relatively great thickness of the outer prismatic layer in the Phylloceratidae can be ascribed to additional adaptations, such as shock absorption over delicate sutures or pigmentation of smooth whorls.

An unexpected feature in the Phylloceratidae is the great diversity of the depth-related parameters of the septa and siphuncle, and the covariation between these parameters (Fig. 8). A modified septal strength index (not that of concave nautiloid septa), suggests that the habitat depth of *Holcophylloceras*, was only about one-half that of *Calliphylloceras* and *Ptychophylleras* (Fig. 8: no. 6 vs. 4 and 5). Significantly, the shell wall has plicate constrictions in *Holcophylloceras* which weakens it, but internal ridges without external grooves in the others. The 10-fold differences in "septal strength index" between the two investigated species of *Phylloceras* (no. 3 a, b) without constrictions, also invite additional research.

## 2.7 Lytoceratina

A sample of 12 Lower Jurassic Lytoceratidae (trend A on Fig. 5, SCHLEGELMILCH 1976; WIEDMANN 1970) showed a significant regression of U on O. The relation of umbilical flutes to whorl shape resembles the trend in the simple-fluted septa of Ceratitina an Ammonitina. Larger *Lytoceras* and the Tetragonitaceae (HEWITT 1985) belong to the multi-fluted group of septa (Table 1):

$$U = 0.015 O + 1.258 \text{ (Lytoceratidae, } r = 0.893)$$

$$\text{Range of } O = 3 \text{ to } 78; \text{ range of } U = 1.25 \text{ to } 2.5$$

Those sceptics who doubt the support function of sutures in the involute Arcestaceae, will note with satisfaction their similarity to the complex sutures of the evolute Jurassic *Lytoceras*. The connecting ring of *Lytoceras jureense*

would have ruptured at about 15 MPa (WESTERMANN 1982); but the unsupported and subcircular whorls of *Lytoceras fimbriatum* (J. SOWERBY) may not have been crushed by membrane stress until a pressure of  $29.6 \pm 4.3$  MPa  $2\sigma$  (at Wh of 51 mm on J1449, a one Table 1). The high sutural complexity of the Lytoceratina (Table 1, including data from SCHINDEWOLF 1961) may reflect the problems posed by bending and extensive sutural shear stresses within the more marginal parts of large and deep-water, anticlastically fluted septa. The high and uniform suture density in *Lytoceras* is consistent with a provisional "Pfaff model", in which most sutural attachments occur in the strongest shelled arcs of deep-water species. HENDERSON (1984) was probably correct in discounting a simple circumferential support role in typical tetragonitids such as *Pseudophyllites*; despite his confusion of stress with pressure.

## 2.8 Cretaceous heteromorphs

The uncoiling of the whorls in some descendants of the Lytoceratida (MIKAILOVA 1982) produced tensile membrane stresses on the inner dorsal shell wall (HEWITT & WESTERMANN 1986, Fig. 8C) and also increased the risk of buckling. The complex suture of the torticone *Turrilites* reflected the effect of external tensile membrane stresses, while the simple suture of orthoconic *Baculites* was related to axial bending stresses and compressive membrane stresses. The ridge of fibrous aragonite seen in *Spirula* (HEWITT & WESTERMANN 1986, Fig. 8C) illustrates the problem of dorsal tension solved by coiled heteromorphs.

One of the larger coiled whorls of *Hoploscaphites plenus* (MEEK) would have been crushed at a pressure of  $8.36 \pm 1.32$  MPa ( $2\sigma$ ) without support from the weak ribs and simple ammonitic sutures (K76, c, Table 1). The thick umbilical wall of the final uncoiled whorl would not have been fractured until a pressure of  $10.58 \pm 1.07$  MPa ( $2\sigma$ , b, Table 1). The adult siphuncle would have ruptured at a pressure of about 4 MPa (WESTERMANN 1982). An unsupported, inner tensile arc of *Didymoceras* (b, Table 1) would have been ruptured by membrane stress at a pressure of about  $17.1 \pm 1.2$  MPa ( $2\sigma$ ) and contain a siphuncle which would have ruptured at pressures of less than 6.5 MPa (index of 9). Compressive membrane stresses would have crushed the unsupported outer arc at a pressure of  $33.6 \pm 5.1$  MPa ( $2\sigma$ , a Table 1) and the ribbing ( $R_2 = 2.5$  mm) may have provided further strength, at least against point impacts (i.e. predation).

The "egg-shaped" *Baculites* whorl section would have been crushed by membrane stress at pressures of between 22 MPa (a, Table 1) and 8 MPa (K91; b, Table 1). Some weak ribbing increased the latter estimate towards 12 MPa (c, Table 1). The siphuncle of other *Baculites* specimens (index of 8) would have ruptured at a pressure of 6 MPa (WESTERMANN 1982).

The orthoconic shell wall required septal support to avoid buckling at pressures of 1 or 2 MPa. The axial bending stresses imposed on the similar Ordovician Lituitidae (Nautiloidea), did not require the development of fluted septa.

## 2.9 Ancestral Ammonitina

The Psiloceratidae (C on Fig. 5 and Table 2), which are thought to be the root-stock of the diverse Jurassic and Cretaceous Ammonitina (SCHINDEWOLF 1962, DONOVAN *et al.* 1981), had more complex and closely spaced sutures

than many of the descendant Psilocerataceae (D on Fig. 5 and Table 2) and probably evolved from the Phylloceratina (TOZER 1981) or Lytoceratina (WIEDMANN & KULLMANN 1981). The relationship of U (umbilical lobes) and O (whorl shape) is shown on Figs. 6 and 7. The Eoderocerataceae show a similarly significant correlation of U on O (E on Fig. 5 and Table 2), which recapitulates the trend obtained from the less complex Triassic ammo-

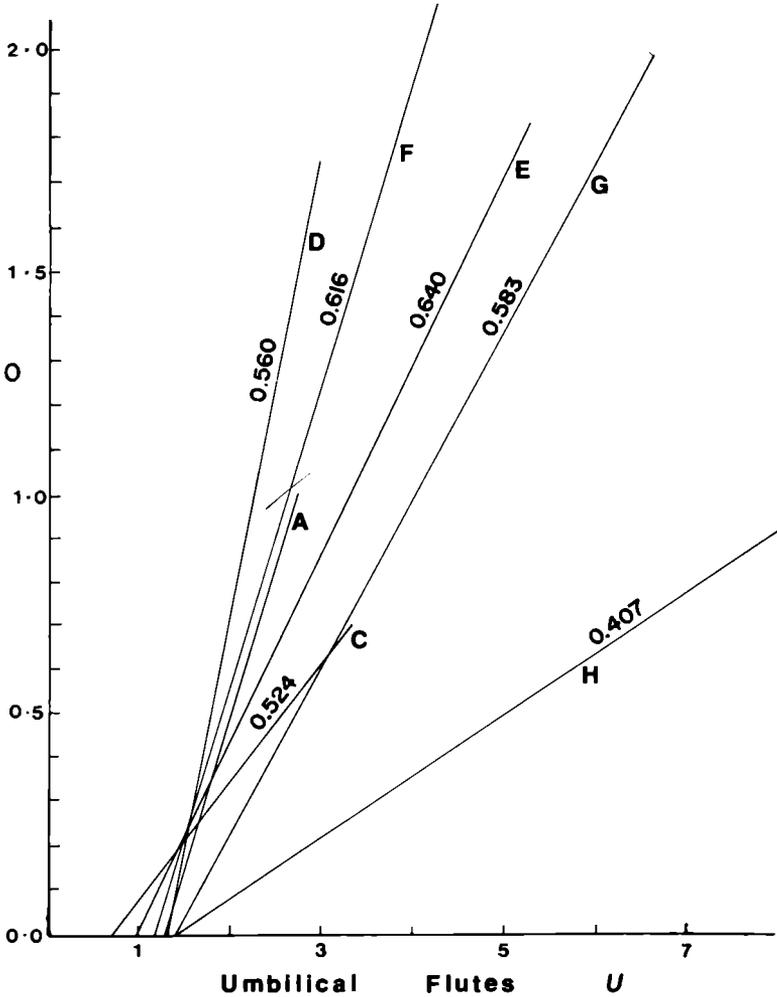


Fig. 5. Regressions of the number of umbilical flutes (U) on the whorl overlap shape ( $O = 100 \text{ Wh}_i / \text{Wb}/2$ ), for Jurassic Lytoceratina (A) and various taxa of Lower and Middle Jurassic Ammonitina (C to H) defined in the text. Regressions in table 2; correlation coefficients indicated.

noid septa. They differed in having moderately complex ammonitic sutures, represented by the relatively simple suture of *Dactyloceras* (Table 1). The early Hildocerataceae are represented by the Lower and Middle Jurassic Arieticeratinae, Harpoceratinae, Hildoceratinae and Grammoceratinae (F on Fig. 5 & Table 2). They showed an increase in the number of umbilical flutes for a given whorl overlap shape and established the multi-fluted and complex sutures as a typical feature of later Ammonitina.

The whorl strengths of representative ancestral Ammonitina were calculated from data presented on Table 1 and compared with revised measurements of the siphuncle rupture depth made on the same whorls (Table 3). It is evident that none of these adult whorls required septal support in order to avoid being crushed at a lower pressure than that required to rupture the siphuncle. The complex suture of the discoidal *Radstockiceras* may prove to be an exception to this rule (GÉCZY 1976, TINTANT et al. 1982). A large and com-

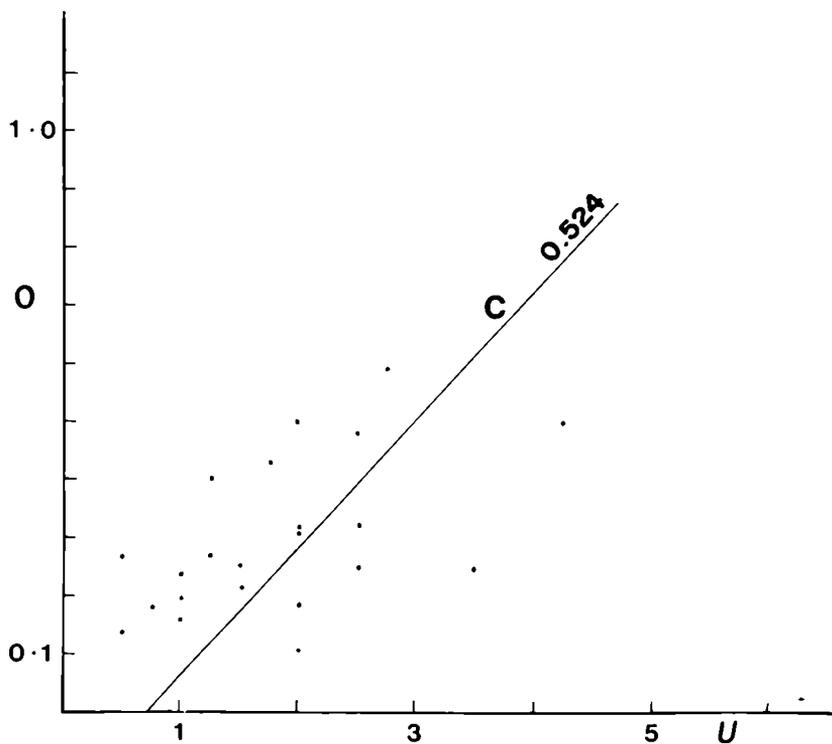


Fig. 6. Data for the regression of U and O for the ancestral Ammonitina (C on Fig. 5 and Table 2), which show a rapid increase in the number of umbilical flutes (U) per unit increase in whorl overlap shape (O). Also note the restricted range of variation in whorl shape within Psiloceratidae from the Hettangian. Correlation coefficient indicated.

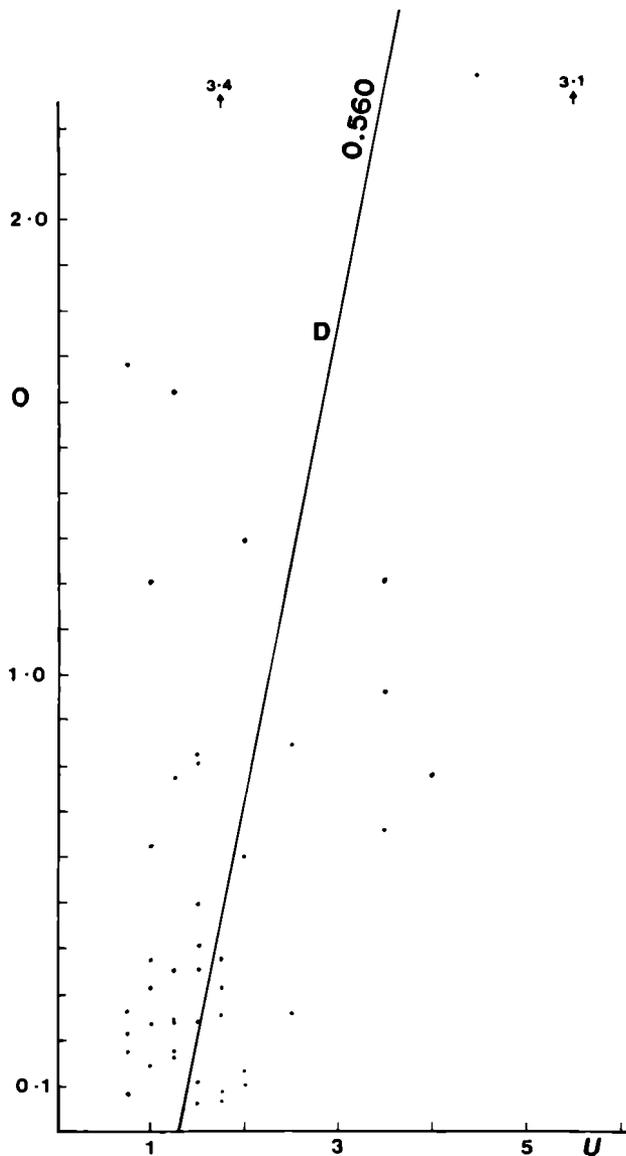


Fig. 7. Data for the regression of  $U$  on  $O$  for the later Psiloceratacea (D on Fig. 5 and Table 2), showing a typical relationship between these two highly variable parameters. This sample of adult and sub-adult taxa represents the Schlotheimiidae, Arietitidae, Echioceratidae and Oxynoticeratidae (Hettangian to Pliensbachian). With correlation coefficient.

Table 2. Regression of umbilical flute number (U) on the whorl overlap shape (O) for Lower and Middle Jurassic Ammonitina. Taxonomic groups (Figs. 5–7) defined in text. Data largely from SCHLEGELMILCH (1976), WIEDMANN (1970), DORN (1935) and WESTERMANN (1954); with examples given in Table 1 and Fig. 3. N = number of adult specimens; r = correlation coefficient (all significant in t-test at 5% probability level).

Taxa	U on O	N	R <sub>coef</sub>	O range	U range
C	0.037 H + 0.731	22	0.524	10 to 50	0.5 to 4
D	0.010 H + 1.302	48	0.560	7 to 340	0.75 to 7.5
E	0.023 H + 0.993	46	0.640	7 to 157	0.5 to 6.5
F	0.015 H + 1.142	37	0.616	24 to 260	0.5 to 6.0
G	0.026 H + 1.411	24	0.583	36 to 194	1.0 to 8.0
H	0.073 H + 1.439	30	0.407	15 to 33	1.5 to 6.0

pressed specimen of *Amaltheus* (*Pseudoamaltheus*) *engelhardti* (d'ORBIGNY) contains a siphuncle with an adult index of 2.8, indicative of a maximum rupture pressure of only  $1.95 \pm 0.42$  MPa ( $2\sigma$ ).

Evolute *Dactyloceras* and compressed *Amaltheus* developed larger bending stresses than the intermediate whorl morphologies. The resulting risk of buckling would be more related to predation and accidents than water depth. But the significant correlations of U on O imply that septal fluting patterns seldom functioned as supports and were largely adapted to resist pressure applied via the body chamber. These Lower Jurassic Ammonitina can be regarded as shallow-water equivalents of the Lytoceratina (TINTANT et al. 1982), with similar septal fluting patterns showing reduced structural complexity. The evidence (BAYER 1977 a, b) for a decline in both sutural complexity and septal spacing in the particularly strong whorls of the shallow-water Arietitidae actually supports the view of WESTERMANN (1975 a) that sutural complexity was a sensitive index of circumferential stress (e.g. *Asteroceras* on Tables 1 and 3).

The effect of transverse, *Argonauta*-like plication (HEWITT & WESTERMANN 1986, Fig. 10A) is illustrated by the typical case of *Psiloceras* (*Caloceras*) *torus* (d'ORBIGNY) with prominent lateral ribs (J403). The maximum possible strength of the ribs was obtained by calculating the tensile membrane stress developed normal to rib troughs. The ribs ( $R_2 = 6.2$  mm) probably fractured longitudinally at a greater depth (c. 10 MPa) than the crushing depth of an unornamented whorl (c. 7.5 MPa) with the same morphology (Table 1). But the addition of tensile bending stresses resulting from buckling of the whorl, to rigid and widely spaced sutural supports, probably neutralised the structural advantage of ribbing. It is doubtful, whether the tentative concept of universal covariation between sutural complexity and ribbing prominence (WESTERMANN 1966: 307), can be applied to many ammonoids.

## 2.10 Multi-fluted Ammonitina

The subsequent sutural evolution of the Ammonitina was determined by the development of multi-fluted septa in the Jurassic Hildocerataceae (DONOVAN et al. 1981). The later Hildocerataceae include evolute *Hamma-*

Table 3. Comparison of the maximum pressures likely to destroy the adult siphuncle and associated whorl arcs of Ammonitina by membrane stresses in excess of the following values: 77 MPa for connecting rings in tension, 114.4 MPa for prismatic outer shell walls in tension (\*), 411 MPa for shell walls in compression as 'short columns'. All the examples ignore internal support from septa and a few are alternative maximum depths based on the local stresses in transverse ribs. Siphuncle strength index and rupture depth of adult siphuncle; whorl max. depth = failure depth of whorl deduced from data in Table 1, for arc see text.

Taxon	Specimen	Arc	Siph. Index	Siph. pressure MPa	Whorl pressure MPa
<i>Psiloceras (Caloceras) torus</i> (ORB.)	J403	a			7.8
<i>Asteroceras</i> sp.	J1439		6.3		14.9
<i>Echioceras</i> sp.	J1477	c*			8.6
		d			12.8
<i>Dactyloceras commune</i> (SOW.)	J18	b	<4.8?	3.6	8.5
	J20	c	<4.8	3.6	8.2
<i>Liparoceras (Liparoceras)</i> sp.	J1450	b		—	7.2
<i>Phlyseogrammoceras dispansum</i> (LYETT)	J531	a	6.5?	5.0	1.1*
<i>P. doermtense</i> (DENK.)	J411	—	6.5	5.0	—
<i>Hildoceras bifrons</i> (BRUG.)	J23	a	10.0	7.7	2.9
		—*	—	7.7	<2.2**
<i>Ludwigia (Brasilia)</i> sp.	J1592	a	—	5.0	9.0
		b*	—	5.0	1.9*
	J1597	—	6	5.0	—
<i>Graphoceras</i> cf. <i>concauum</i> (SOW.)	J1599	—*	9.0	6.9	1.8*
<i>Sonnina espinazitensis</i> (TORNO.)	J1311–3	b	8	6.6	5.6
		—*			<12.0**
<i>Normannites quenstedti</i> ROCHÉ	J1490	a	<3.5	<2.5	14.5
		—*			<20.0
<i>N. orbigny</i> (BUCK.)	J427	c			18.3
		—*			<20.0**
<i>Emileia giebeli</i> (GOTT.)	J1340	a	8.2	6.2	14.6
<i>Macrocephalites</i> sp.	—	d	7.2?	5.5	5.1
		e	7.2?	5.5	6.9
		f	7.2	5.5	8.6
		g			9.3*
<i>Perisphinctes (Dichotomosphinctes)</i> sp.	J1492	a	7.0	5.4	10.3
<i>Virgatosphinctes</i> sp. from Argentine	153V1	1a	10.8	8.3	4.9
		—*			7.4*
<i>Kossmatia bifurcata</i> (AQUIL.)	1535/5	a	8.7	6.7	2.5
<i>Uhligites</i> cf. <i>indopicta</i> (UHLIG)	J1974c	—	11.8	9.1	—
<i>Oxerites</i> sp. from Cutch		a	12.0	9.3	2.8
<i>O.</i> sp. from Chile	7903312	b	12.0	—	4.0
<i>Placentoceras whitfieldi</i> HYATT	K490	a		2.0	3.3
	K118	b		2.0	7.5
	K191	—	2.5	2.0	—

*toceras* ( $U = 4$ ,  $O = 79$ ) and compressed genera, e.g. *Sonninia* and *Ludwigia* s.l., that would have required septal support to descend to the moderate depth implied by their siphuncles (Tables 1 and 3). This group shows a significant correlation of umbilical flutes  $U$  on overlap shape  $O$  ( $G$  on Fig. 5 and Table 2) which implies a shift towards the multi-fluted septa of the Phylloceratina. Late ludwigias (e.g. *Brasilia*, *Graphoceras*) created great hydrostatic problems by evolving a smooth concave-out tensile arc near the umbilicus (Tables 1 and 3). The compressed whorl and numerous saddle-flutes of *Dorsetensia* (Sonniniidae) were illustrated by PFAFF (1911).

BAYER & MCGEE (1984) report that these ammonites developed oxyconic whorls with reduced sutural complexity in shallow-water geological facies.

The evolute and transversely ribbed Stephanoceratidae show an ever faster rate of increase of  $U$  on  $O$  ( $H$  on Fig. 5 and Table 2, Stephanoceratinae and Cadomitinae) and developed high sutural complexity (ISC) in the strong-walled and shallow-water *Stephanoceras* and *Zemistephanus* (Table 1 and 3). The related Otoitidae and Sphaeroceratidae had smoother and more involute macroconchs, with a high if declining  $U/O$  ratio and moderate ISC (Table 1). It is possible that the higher surface to volume ratio of these whorls ( $X/\sqrt{K}$ ), permitted a reduction in sutural complexity. *Mayaites* (*Epimayaites*) *lemoini* SPATH (THIERRY 1980) completed the homeomorphy with Triassic *Cyclolobus* and *Joannites*. The similar whorls of *Macrocephalites* had a complex suture that was sometimes required to support the lateral shell wall against hydrostatic pressure (Tables 1 and 3). The deep umbilicus would have fractured at the depth required to crush the lateral wall ( $f$  and  $g$ , Table 1), but this was nearly twice the rupture depth of the adult siphuncle (Specimens on Table 3 from the K. SIDDIQUI collection from Cutch, India).

The Perisphintaceae were long-ranging descendants of the Stephanoceratidae, often with complex sutures and multi-fluted septa (e.g. DRUSCHITS et al. 1977a). Tithonian *Virgatosphinctes* and *Kossmatia* had evolute, subrectangular whorl sections that probably required support from their septa, as well as from their strong transverse ribbing. But the covariation between sutural complexity (ISC) and whorl shape ( $X/\sqrt{K}$ ) in *Leopoldia*, *Olcostephanus* (RICCARDI et al., 1972) and *Collotia* (Table 1, after CARIOU 1980) suggests that their sutural complexity was largely determined by the "PFAFF model".

In contrast, the deep-water and compressed Oppeliidae (Haplocerataceae) retained the vital support function of the septa seen in some Hildocerataceae (e.g. HEWITT & WESTERMANN 1986, Fig. 6). They had multi-fluted septa and evolved into diverse post-Lower Cretaceous Ammonitina (Desmocerataceae, Hoplitaceae, Acanthocerataceae), which largely reverted to the septal functions of the older Ammonitina. These Cretaceous septal sutures (Fig. 3) show a small increase in  $U$  with  $O$ , structural complexity and a tendency to be associated with transverse *Argonauta*-like ornamentation.

The more compressed Upper Cretaceous taxa include the large, shallow-water hoplitid *Placenticerus whitfieldi* HYATT, and the smaller pseudoceratite *Metaengonoceras inscriptum* HYATT. The multi-fluted septa of *Placenticerus* resemble those of *Phylloceras*; but *Placenticerus* apparently lived in shallow water (< 2 MPa) which did not impose a crushing load on the whorls (Table 3). The linked ceratitic sutures of *Metaengonoceras* may have supported a flat whorl to a theoretical pressure of 20 MPa and recall the functions of chain mail. It is likely that their strength was used to resist predation and buckling phenomena in shallow-water. Even the unsupported shell wall may not have been crushed until a pressure of 5 MPa, probably well below their habitat.

References to other taxa on Table 1 are given by HEWITT (1985). The variable axial curvature of saddle-flutes in compressed *Placenticerus*, *Coahuilites* and *Sphenodiscus* (KENNEDY & COBBAN 1976, pl. 6-7) may be a near-shore anomaly. The unphosphatised connecting rings of *Placenticerus* ("*Platylenticeras*" K501) illustrated by HEWITT & WESTERMANN (1983), would have ruptured at a pressure of less than 3.4 MPa.

### 3. Discussion

One popular solution to the difficulty of interpreting septal and sutural functions (see reviews in RAUP & STANLEY 1971: 172-181, WESTERMANN 1971: 15-22, WIEDMANN 1972: 591-594, VALENTINI & FINKS 1974, SEILACHER 1975: 284, KENNEDY & COBBAN 1976: 23-27) is to accept all the previous speculations on this topic and elevate them to independent variables within an intractable case of mosaic evolution. But only one of these explanations appears valid.

The periodic nature of septum growth precludes the hypothesis of SPATH (1919: 30) and HENDERSON (1984), that septal fluting served to aid the attachment of muscles to the septum. There is only a limited distribution of muscle scars on the shell wall of ammonoids and *Nautilus* (JORDAN 1968, BANDEL & SPAETH 1983). The mantle fluting mechanism proposed by BAYER (1977a, 1977b) is inconsistent with the mode of growth (HEWITT 1985) and buoyancy adaptations of cephalopods (BLIND 1980, WARD et al. 1981).

WESTERMANN (1971, 1975b) rejected speculations on the function of fluted septa for removal of cameral fluids in ammonoids (MUTVEI 1967). Rapid diffusion could have occurred via the inner prismatic layer and "pellicles" on the shell wall to the ventro-marginal siphuncle. Ammonitic sutures, like *Sepia* intracameral walls (HEWITT & WESTERMANN 1986, Fig. 9), extended this diffusion pathway so as to isolate a ballast of cameral liquid. The cameral ballast hypothesis of HOUSE (1975:483; 1981:9), KULICKI (1979) and WARD (pers. commun.), possibly involved relatively slow diffusion of fluid over the

septum from the folioles and lobules; or storage in a "septal pellicle" with a capacity for strong swelling (BANDEL & SPAETH 1983). The ontogenetically increasing ratio between the volume of cameral liquid and the area of siphuncular epithelium (WESTERMANN 1971: 27, WARD 1982) seems inconsistent with this paradigm. COLLINS et al. (1980) and WARD et al. (1981) imply it was more advantageous for ammonoids to increase their growth rate by reducing the length of diffusion pathways in large whorls.

Hypotheses involving the constructional advantages of thin, fluted septa probably fail due to the similarly slow growth rates of ammonoids and *Nautilus* (WESTERMANN 1971:29, ZAKAROV 1977, WARD et al. 1981). *Phylloceras* and *Dactyloceras* foliole shape is related to structural factors (HEWITT & WESTERMANN 1986, section 2.5), as well as the reversal of the orientation of their last septa.

SEILACHER (1975) seems to imagine that the planar and anticlastic form of the organic septal template would not buckle under compressional loading by pressure. We propose that ammonoids resembled *Sepia* (BANDEL & BOLETZKY 1979), in having a chitinous and proteinaceous gel instead of the cameral water secreted behind the body of nautiloids (WARD et al. 1981). This *cameral matrix* had the same density as the body tissue and would have added a stiff support for the delicate fluting of the posterior mantle epithelium during the forward movement of the soft parts. Subsequently it would be dehydrated to the cameral membranes sometimes preserved by pyrite or phosphate within ammonoid chambers.

The provisional 'Pfaff model' of HEWITT & WESTERMANN (1986) is inappropriate for ammonoids showing a variation in sutural density within each whorl, that was inversely proportional to the local wall strength (HEWITT 1985). The most differentiated sutures occur in the Phylloceratina and other weak-shelled taxa, in which the septa had a circumferential support function ('Westermann model'). In deep-water taxa with flattened whorls, the differentiation consisted of phylloid folioles situated on saddles showing ceratitic differentiation (e.g. *Phylloceras*), while in shallow-water taxa it produced linked pseudoceratitic sutures (e.g. *Metaengonoceras*). The discussion of ammonoid septa presented by HENDERSON (1984) was largely based on the negative thesis that both the shell wall and the septa were too strong.

Analogies with the laterally supported saddles of building terminology, suggest that the amplitude of purely self-supporting saddle-flutes was proportional to internal bending stresses and inversely proportional to internal shear stresses. The circumferential load produced additional axial bending stresses along the ammonoid saddle-flutes. It is, however, clear from the present study that these bending stresses were not so large as to preclude the use of flutes as

internal supports (cf. BAYER 1977a, 1977b). Compressed whorls of moderately deep-water Phylloceratina, Hildocerataceae and Haplocerataceae required internal septal support against hydrostatic pressure; as did some quadrate whorls of Perisphinctaceae and other taxa. This implies that the fluted septa of other ammonoids with stronger whorls supported the shell wall during accidents or predation (point loads). These ammonoids were preadapted to the deeper water habitats imposed on lineages by offshore migration during regressions, or made available to them in transgressions. Any periodic speciation events favoured the evolution of multi-fluted septa with complex sutures, which were only partially retained in descendant shallow-water taxa such as *Asteroceras* and neoceratites. The size-related, spring-like support from septa enabled ammonoids to show a wide range of intraspecific variation in streamlining and ornamentation, without showing much covariation in ribbing, shell thickness or septal spacing.

The significant correlations of umbilical flute numbers on whorl overlap shape (U/O; Figs. 3, 5–7) demonstrates that typical adult Mesozoic ammonoids have about the same number of saddle-flutes for the same degree of whorl overlap, regardless of their sutural complexity and phylogenetic history. A minority of unrelated taxa show a greater rate of increase in fluting per increase in whorl overlap. These multi-fluted septa occur in taxa adapted for the 'Westermann model'; but also include enigmatic extinction-prone taxa, in which the sutural zone was not radial, i.e. aligned within the plane of the hoop stress in the whorl (*Cyclolobus*, *Joannites*, *Pinacoceras*, *Epimayaites*). There is evidence of a simple relationship between septal and siphuncular strength in typical Mesozoic ammonoids (Fig. 8). It is sufficient to consider the 'hybrid Pfaff' and 'Westermann models' as a single unifying hypothesis.

The absence of quasi-hemispherical septa in the strong and subcircular whorls of deep-water *Lytoceras*, implies that the Devonian evolution of fluting was an irrevocable process, in which the similar sized and depressed septa in the first whorl (ammonitella) became more fluted during ontogeny and phylogeny (SCHINDEWOLF 1954: 229). This could mean that there were restrictions on mantle resorption in ontogeny (HEWITT 1985). An ontogenetic return to geometrically simple hemispherical septa, could have also required a new gene regulatory mechanism (see RAFF et al. 1984 for an echinoderm analogy) suppressing gel production and fluting of the posterior epithelium.

If *Lytoceras* sutures are interpreted as necessary adjustment to a basically unsuitable fluted septal 'design', then there must have been strong selection pressures requiring the retention of a circumferentially stressed, depressed whorl section in the ammonitella. This embryonic first whorl (DRUSCHITS et al. 1977b, KULICKI 1979, BANDEL et al. 1982) contained nacreous septa formed (or at least, emptied) after hatching. The ammonitella was smaller than the embryonic *Nautilus* (1 mm versus 25 mm) and may have been incapable of moving through, or rupturing a large protective egg capsule.

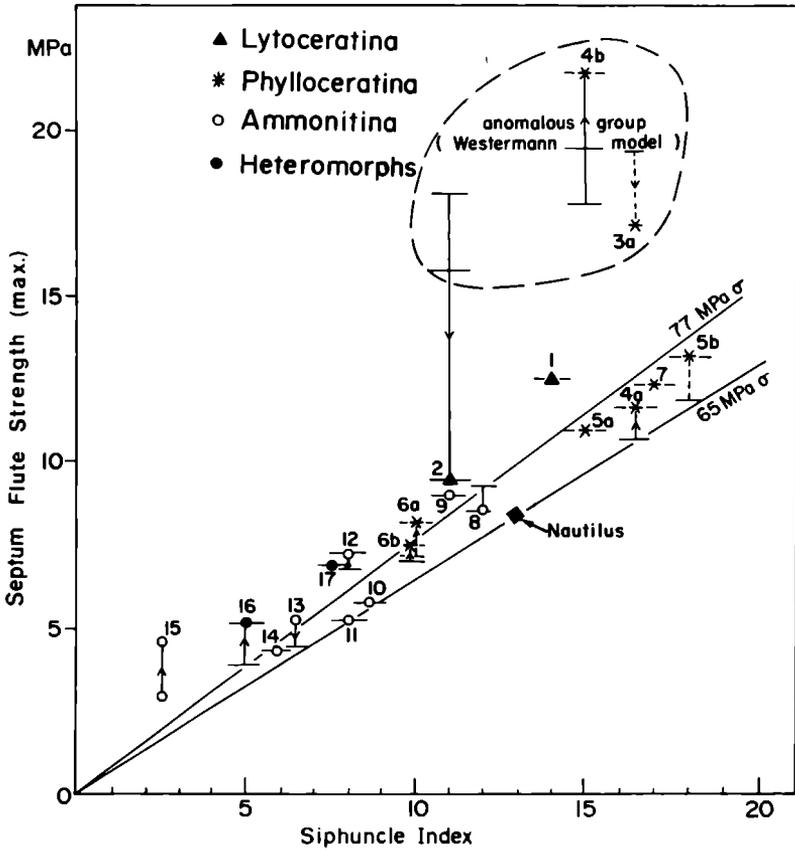


Fig. 8. Correlation between ammonoid siphuncle and septal flute strength indices based on 21 adult taxa - The septal whorls index is  $P = 193 \text{ MPa}/0.5 \text{ Wb}/d_s$  in compressed whorls and  $P = 193 \text{ MPa}/0.5 \text{ Wh}/d_s$  in depressed whorls is only a tentative and approximate estimate of the stresses in anticlastically fluted septa, but does correspond to the stress implied by the maximum recorded tensile strength of the connecting ring in *Nautilus*. [The pressure implied by the siphuncle strength index  $P = 77 \text{ MPa}/(1/0.02 \text{ siphuncle index})$ .]

Lytoceratina: 1, *Lytoceras* (J1778); 2, *Pseudophyllites* sp. (K80). Phylloceratina: 3a, *Phylloceras* cf. *plicatum* (C1-7); *P. heterophyllum* (J1488); 4, *Ptychophylloceras* cf. *galoi* (J2026g); *P. plasticum* (C4-8); 5a, *Calliphylloceras malayanum* (J2005g); 5b, *C.* cf. *heterophylloides* (J1280); 6a, b, *Holcophylloceras* cf. *ultramontanum* (J155, J133); 7, *Haplophylloeras strigile* (J2034L). Ammonitina: 8, *Canadoceras newberryanum* (K1069); 9, *Pachydiscus* sp. (K986B); 10, *Sonninia espinazitensis* (J1311-3); 11, *Grammoceras doerntense*; 12, *Erycitoides howelli* (?J1241); 13, *Ludwigia (Brasilia) gigantea* (J1597); 14, *Emileia giebeli* (J1340); 15, *Placentoceras whitfieldi* (K36). Ancyloceratina: 16, *Scaphites hipocrepis* (K66); 17, *Baculites compressus* (K658).

This suggests it may have been protected by a small form of the bird-like egg-shells found in cirromorph octopods (BOLETZKY 19827, OR 1 MM DIAMETER GELATINOUS EGGS LIKE *Spirula* (BRUNN 1943, pl. 2. Fig. 14); the only living cephalopod with an ammonoid-like protoconch, caecum and prosiphon. The absence of an ammonoid-like proseptum in *Spirula* may be ascribed to the very short length and open coil of the 'body' chamber' in this entirely internal shell (HEWITT & WESTERMANN 1986, Fig. 8C). A small egg would have permitted ammonoids to develop a more r-selected evolutionary strategy than nautiloids, aiding survival as a micromorphic deep-water and cosmopolitan lineage during ecological crises.

The embryonic body chamber surrounding the ammonoid protoconch typically has a depressed and crescentic whorl section, which maximised body size in the spherical egg (Fig. 2-3). The highly fluted and mechanically weak proseptum (BIRKELUND 1981), which is the only embryonic septum known in typical ammonoids, need not have been exposed to hydrostatic pressures applied via the body chamber. This situation could have resulted if buoyant eggs were laid in a floating raft or in shells (as in *Argonauta*), or through the delayed evacuation of water. The fluted morphology of the proseptum is interpreted as the effect of circumferential loads imposed on the radially oriented orifice of the protoconch after the ammonitella had hatched from the egg. Similarly, the fluted morphology of the true septa which subsequently fill the body chamber of the ammonitella, may be ascribed to an uneven circumferential load, imposed by the egressing umbilical seams of the second, more rounded whorl on the shallow-arched venter of the first (embryonic) whorl (Fig. 3A; WESTERMANN 1956, Fig. 2). The fluted 'design' of early nacreous septa is also related to the depth limitations imposed by the need for a large transverse curvature radius ( $R_1$ ) on sub-hemispherical septa within depressed whorls. Thus both the 'Westermann model' and the 'Pfall model' favoured the maintenance of a fluted septum with ammonoids in offshore breeding highly depressed embryonic shells. This hypothesis seeks to limit the "orthogenesis" of Lamarkian Palaeontology opposed by HALDANE (see HUXLEY 1974: 507) and the mysteriously "complex system of pleiotrophic genes" postulated by WIEDMANN & KULLMANN (1981: 216), so as to set no limits to the rational mechanical interpretation of ammonoid suture lines.

## Übersicht

Die traditionelle Debatte über die Funktion von komplizierten Suturlinien in Ammoniten behandelt die relative Wahrscheinlichkeit und gegenseitige Ausschließlichkeit von allgemeinen Funktions-Modellen. Beispiele sind die Notwendigkeit von Mantel- oder Muskelanheftung und periodischer Septum-Herstellung, die mechanische Stärke des ausgebildeten Perlmutter-Septums, und seine mögliche Rolle als Trennwand zwischen Ballast-Ladungen von Kammerflüssigkeit. Keines dieser allgemeinen Modelle machte Aussagen über die komplizierte und doch konservative

Form von Ammoniten-Suturen (Lobenlinien), und keine noch so weithergedachte Vereinigung verschiedener Adaptationsmodelle erklärte die Form-Gegensätzlichkeit, veranschaulicht durch Lytoceraten und Phylloceraten. Die weitere Analyse des mechanischen Modells hat aber jetzt viele dieser Schwierigkeiten gelöst.

Im Gegensatz zu früheren Angaben haben viele adulte Ammoniten eine dickere Phragmokon-Wand als gerade und aufgerollte Nautiloideen. Die hemisphärischen Septa und geraden Suturen von orthokon Nautiloideen waren gut für das „Pfaff-Modell“ geeignet, in dem der Wasserdruck hauptsächlich durch den Weichkörper übertragen wird. Dieser Bauplan hatte auch den Vorzug, während des Wachstums ohne Zunahme der Suture-Zerschlitzung vergrößert werden zu können. Der endgültige Verlust hemisphärischer Septa in der frühen Evolution der Ammonitiden kann nicht mit irgend einem Merkmal der adulten Morphologie erklärt werden. Er scheint vielmehr durch die Entwicklung eines platten Wohnkammer-Querschnitts im kleinen, sphärischen Ei begründet zu sein. Die Fältelung der juvenilen Suturen entspricht demnach dem „Westermann-Modell“, in dem die Septa im wesentlichen einem hydrostatischen Umfangedruck ausgesetzt waren und die von der folgenden Windung ungleichmäßig belasteten Schalenwand stützten.

Viele mechanische Folgerungen des „Pfaff-Modells“ sind verborgen unter theoretischen Problemen der Sattelfalten. Die Stützrolle dieser Strukturen kann etwas einfacher aus Ingenieur-Prinzipien abgeleitet werden und besser verstanden werden durch Experimente an der schwachen Außenschale des *Nautilus*-Phragmokons. Die halbrunde Pfeiler-Falte (pillar flute), welche die *Nautilus*-Schale unterstützt, hat wahrscheinlich die kritische Wassertiefe verdoppelt, bei der die Schale durch den hydrostatischen Druck zerbrechen würde; aber die Pfeiler-Falte kann auch den Bruch dieser Schalenwand unter Zugspannung verursachen, falls die steifen Firsten und Stützen, d. h. die Lateralloben, zu weit auseinander stehen. Die zunehmende Komplikation adulter Ammonoitiden-Suturen diente zur Abstands-Verringerung zwischen den internen Stützelementen, während die Achsbiegung der Sattelfalten zusätzlich die externen Spannungen durch Verringerung der Steifheit reduzierte. Die damit verbundene Implosionsgefahr, hervorgerufen durch die zusätzlichen Biegungs- und Membranspannungen in den dünnen, nach außen konvex gekrümmten Bögen des letzten Septums, war durch die halbkreisförmige Aufblähung der Sättel und Foliolen reduziert.

Das Ausmaß der internen Stützfunktion der Septa während des Wachstums hing hauptsächlich vom (1) adulten Phragmokon-Querschnitt und (2) von der Wassertiefe ab. Wegen der Sekundär-Funktionen des adulten Phragmokons, (z.B. als Behausung, Strömungskörper und Maskierung), waren beide Faktoren größtenteils unabhängig, was zur Variabilität der Suture beiträgt. Zum Beispiel unterschieden sich die adulten Phylloceratina von adulten Lytoceratina des gleichen Tiefwasserbereiches durch die Notwendigkeit, die Schalenwand intern abstützen zu müssen. Der Unterschied in der Maximal-Tiefe von Phylloceratina und den ähnlich komprimierten Ammonitina wie *Placenticas*, war groß genug, um gewisse Phänomene wie Suture-Vereinfachung durch Verringerung der Innen-Abstützung zu erklären. Gehäusegröße ist ein anderer wichtiger Faktor, weil hier Biegungsspannungen in der Schalenwand oder im gefalteten Septum größer werden können als die Membranspannungen. Trotz der offenbaren Vielfalt von ammonitischen Schalenformen haben wir festgestellt, daß eine in verschiedenen Familien oder Superfamilien-signifikante Korrelation besteht zwischen der Anzahl umbilikaler Sattelfalten (Loben und Sättel) und dem Querschnitt der überlappenden Windungen. Taxa, welche ihre Septa als interne Stützen zu benutzen tendierten, werden durch eine größere Zahl von Sattelfalten pro ähnlichem Umschlag, sowie durch Asymmetrie im Profil der Lobuli und Foliolen charakterisiert.

Wir postulieren, daß der Ursprung der Septalfältelung auf die Evolution einer flachen embryonalen Wohnkammer in einer kleinen, sphärischen Ammonitella zurückzuführen ist;

das kleine Ei erbaute eine  $r$ -Modus Selektions-Strategie. Die ontogenetische Beibehaltung eines gefalteten hinteren Mantels weist auf die Schwierigkeit hin, diese Strukturen zu resorbieren. Die Entwicklung bevorzugte daher erhöhte Marginalfaltung, sodaß die Septen nicht unter dem hydrostatischen Druck von der Wohnkammer her zerbrechen. Mehrere wichtige Ammonoiden-Gruppen hielten die marginale Stützfunktion aber während der gesamten Ontogenie aufrecht. Diese ammonitische Suturen ermöglichen den Ammonoideen, eine größere Formenvielfalt in der Schalenform zu erreichen und sich schneller an Tiefegebundene ökologische Krisen zu adaptieren, als der mechanisch „steifere“ und phylogenetisch konservative Bauplan der Nautiloideen.

### Acknowledgments

Dr. M. R. CLARKE F. R. S., Dr. R. H. MAPES, Mr. K. SIDDIQUI and Dr. R. JORDON provided material. Dr. K. BANDEL, Prof. J. D. CURREY, Dr. R. VICENCIO, Prof. M. R. HOUSE, Dr. Y. KANIE, the late Dr. T. J. M. SCHOPF and Dr. YI-GANG WANG answered queries or provided discussion. Dr. D. S. WEAVER of the Department of Mechanical Engineering at McMaster University helped with the experiments on models and *Nautilus*. Drs. H. HORVATH and D. S. WILKINSON made available laboratory facilities. CHRIS ROSE and GEROLD WESTERMANN helped with the *Nautilus* study. The research was funded by a grant from NSERC to G. E. G. WESTERMANN. Dr. P. WARD read the manuscript. Some photographs were taken at Hull University during a N.E.R.C. studentship supervised by Prof. M. R. HOUSE.

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Bei der Tübinger Schriftleitung eingangen am 10. Januar 1986.

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