

Function of Complexly Fluted Septa in Ammonoid Shells

I. Mechanical Principles and Functional Models

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With 10 figures in the text

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Abstract: Ammonoid septa were adapted to resist hydrostatic loads applied via the body chamber ("PFAFF model") and the weak shell wall of certain taxa ("WESTERMANN model"). Thus there are at least three independent variables controlling the influence of these two functional models on a particular ammonoid septum, namely the habitat depth (hydrostatic pressure), whorl profile (membrane stresses in the shell wall without septal support) and the absolute size of the whorl (bending stresses in the shell wall and fluted septum).

Key words: Ammonoids, thin shells, saddles, Jurassic, septa, sutures.

Zusammenfassung: Ammoniten-Septen waren an die hydrostatische Belastung angepaßt, die über die Wohnkammer (Modell von PFAFF) und/oder die Außenschale (Modell von WESTERMANN) wirkte. Drei Variablen übten hier Einfluß aus: die Habitat-Tiefe (hydrostatischer Druck), das Windungsprofil (Membranspannung in der Schalenwand bei bestimmtem Wasserdruck, ohne Septen-Verstrebung) und die absolute Größe der Windung (Krümmungs-Spannungen in Septen und Schalenwand).

I. Introduction und terminology

Part 1 of this paper concerns the mechanical principles and functional models, new and old, concerning complexly fluted ammonoid septa. Part 2 will test the functional aspects of septal evolution, review different hypotheses relating to the function of sutures, and draw some conclusions.

Although it is debatable whether a complex ammonoid suture (ARKELL 1957 b) was a purely mechanical adaptation, there is no reason to suppose that ammonoid phragmocones did not function as a fixed volume hydrostatic apparatus like Recent phragmocones (DENTON 1974). This implies that they tended to be minimum-weight structures. According to Maxwell's Lemma (WAINWRIGHT et al. 1976: 289) the most efficient design would be

composed of either tensile or compressive elements, with bending stresses reduced to a minimum. A single large spherical chamber would resist hydrostatic pressure in compression and could operate at almost any depth in the ocean; but would not serve the hydrodynamic functions of phragmocones. It would also be impossible to grow without vertical migration and resorption events. A variation in adult implosion depth from 200 m (*Placenticeras*) to 1700 m (*Lytoceras*), is implied by the maximum tensile strength recorded from the connecting rings of adult *Nautilus* (77 MPa, calculated from CHAMBERLAIN & MOORE 1982) and the structure of cylindrical siphuncles of ammonoids (WESTERMANN 1971; 1982). The interpretations presented here imply that the suture morphology was adapted to avoid the implosion of the phragmocones at these water depths (WESTERMANN, 1956, 1958, 1965, 1975).

The mechanical properties of nacreous phragmocones had the following approximate values: crushing strength = 411 Mpa, tensile strength (Modulus of Rupture) = 193 MPa, tensile strength of outer prismatic layer of shell wall = 109 MPa, Young's Modulus (E) = 47 GPa, Poisson's Ratio (ν) = 0.31. The tensile strengths are based on bending tests on the *Nautilus* shell wall by CURREY (1976 & pers. commun. 1982) and a new measurement of 187 MPa for the nacre. The E and ν parameters are mutually consistent estimates made from studies of *Nautilus* septa with strain gauges and are still uncertain. A measured E value of 47 GPa (CURREY 1976) is quite consistent with septum strain gauge data when ν is 0.3. The maximum-stress theory appears applicable to hydrostatic implosion of phragmocones (DEN HARTOG 1949: 77). Specimens are housed at McMaster University.

Four arguments may be raised against these general assumptions. The first can be based on the speculation that some growth stages had a last septum which was not stressed by hydrostatic pressure. This could occur in a water-filled benthic growth stage, as seems likely in the case of embryonic *Nautilus*, or surface dwelling gas-filled plankton. Given a strong shell wall, the main (unknown) selection pressure on conservative embryonic goniatitic sutures would then have acted before evacuation of water during chamber growth.

Secondly, constructional constraints may explain the occurrence of apparently poorly designed, concave-out hemispherical septa in nautiloids (WAINWRIGHT et al. 1976: 263; Westermann 1977). It seems unwise to base initial interpretations of ammonoids on the constructional models of ARKELL (1957 a: 243), SEILACHER (1975), WESTERMANN (1975: 247–250) and BAYER (1977 a, b). The loss of hydrostatic functions, or the increase of cameral gas pressure, would have involved the loss or calcification of their thick "horny tube". Judging from the coleoids, it would also have involved the replacement of the ancestral lenticular nacreous microstructure by a wide variety of flexible fibrous, granular or chitinous materials (Fig. 1). Microstructural descriptions of ammonoids and nautiloids (see reviews by BIRKELUND 1981 and DRUSCHITS & DOGUZHAYEVA 1981) show that the ammonoid microstructures are nearly identical to those of *Nautilus* and are an even more conser-

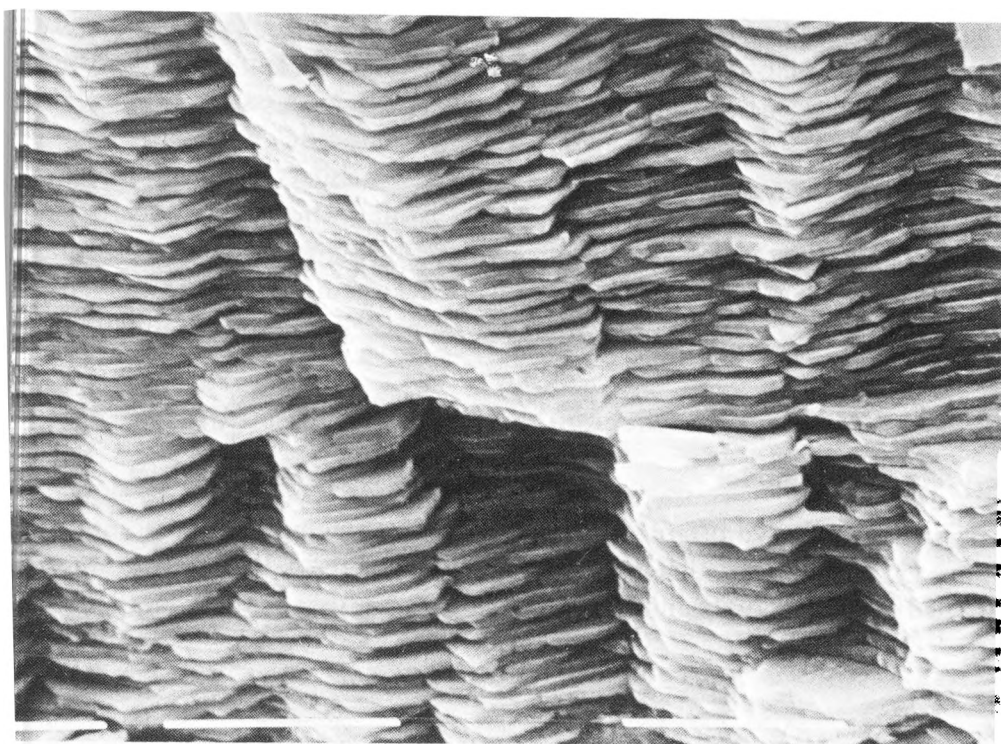


Fig. 1. Fractured longitudinal section of the septal neck of a Jurassic *Haplophylloceras* showing aragonite columnar nares (J2034L, Tithonian of Indonesia, scales 1 μm).

ervative character than early sutural morphology. This observation also contradicts the third possible objection to our assumptions; namely that *Nautilus* and ammonoid shell material had fundamentally different mechanical properties.

The fourth critique starts from the view of GOULD (1977: 229) that ammonitic sutures resulted from an increase in allometry, reflecting an unspecified selective advantage in evolving a complex suture. If that complexity was a strategy for reducing bending stresses, then the selection pressure could have included the addition of unpredictable stresses due to accidents, predation, constructional flaws and superimposed internal sutures, to the hydrostatic stresses applied to the exposed part of the last whorl. The hydrostatic implosion depth of *Nautilus* is at about 800 m while the maximum habitat depth is at 500–600 m (WARD et al. 1984). If randomly occurring point stresses were added to the maximum bending stresses developed mid-way between the sutural supports of the shell wall, the most efficient design for a “safety factor” would not be the same as for higher hydrostatic pressure. The reduction of the bending stresses by a well designed system of closely spaced sutural supports, provides a more efficient “safety factor” than a uniform increase in shell thickness. The resulting trend towards sutural complexity would be more important in thin or flat whorls

than in stronger whorls, or in deeper water, *Nautilus*-like phragmocones. Since one source of selection pressure is point stresses applied by vertebrate predators (MAPES & HANSEN 1984, KAUFFMANN & KESSLING 1960), it is possible that the change from goniatitic to ammonitic sutures in ontogeny and phylogeny was not ultimately related to habitat depth or shell wall geometry. But since this speculation could explain the anomalies of sutural evolution, it supports a general hydrostatic model. None of the arguments of HENDERSON (1984) can be accepted as evidence against the general paradigm employed here, although his critique was necessary and stimulating.

2. Potential mechanical functions of sutures

2.1 The "Pfaff model"

The general hydrostatic interpretation of phragmocones presented by PFAFF (1911) assumed that they were adapted to resist hydrostatic pressure applied via the body chamber to the last gas chamber. In the "Pfaff model"

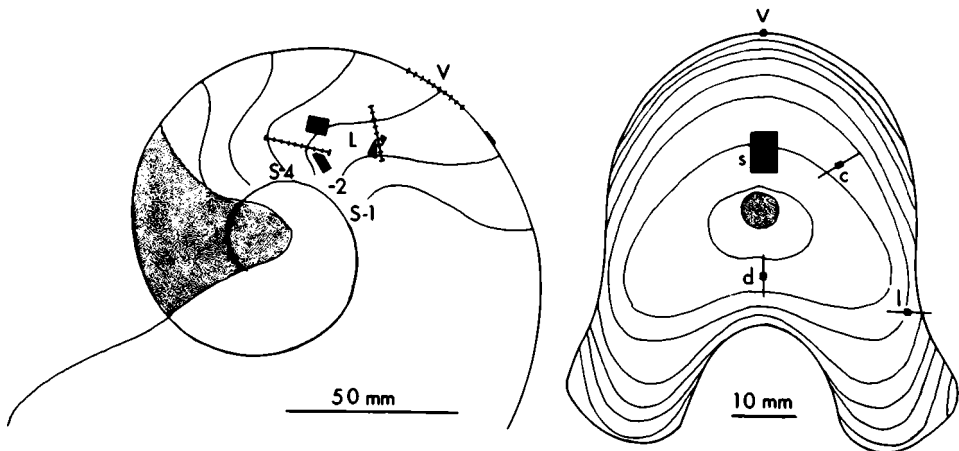


Fig. 2. Lateral external view with septal sutures (left, numbered from last) and contoured adult septal surface (right, after R. VICENCIO unpublished) of *Nautilus* showing the position of strain gauges. The two series of 0.8 mm square gauges on the lateral lobe (L) are compared with the strain recorded in the ventral series (V) on the same shell (Fig. 3). Isolated larger gauges recorded the strain within the septa of another specimen, in which a convex hemispherical septal surface was exposed to a hydrostatic pressure of 0.6849 MPa. The compressive strain in the axis of the lateral pillar-flute (-1.1128×10^{-4} , 1 on last septum), contrasts with equivalent strains transverse to the axis (-2.443×10^{-5} , d) and in the exposed hemispherical region of the adolescent and last septum (-2.31×10^{-4} at c, $+1.30 \times 10^{-4}$ at s after SAUNDERS & WEHMAN 1977). KANIE & HATTORI (1983) report equivalent tensile strains ($+1.710 \times 10^{-4}$, $+1.203 \times 10^{-4}$) in the more ventral region of the last septum of other shells. The new strain measurements, made immediately after the application of hydrostatic pressure in repeated runs at intervals of more than half an hour, avoid problems posed by anelastic reductions in recorded strain. Results of the largest gauges on the shell wall (SAUNDERS & WEHMAN, 1977) contradict the large strains erroneously reported from live *Nautilus* by KANIE & HATTORI (1983 table 1; gauge projected on our series right of L).

the internal septa could have been resorbed without decreasing the implosion depth. It does not explain the generally close spacing of ammonitic suture-zones. Evidence that the relatively strong outer shell of *Nautilus* can remain unbroken due to a chain reaction of septum implosion [RAUP & TAKAHASHI 1966], is refuted by later implosion experiments such those of SAUNDERS & WEHMAN (1977). Our experiments on *Nautilus* shells confirmed that the strain in the flattened shell wall overlying the lateral lobe

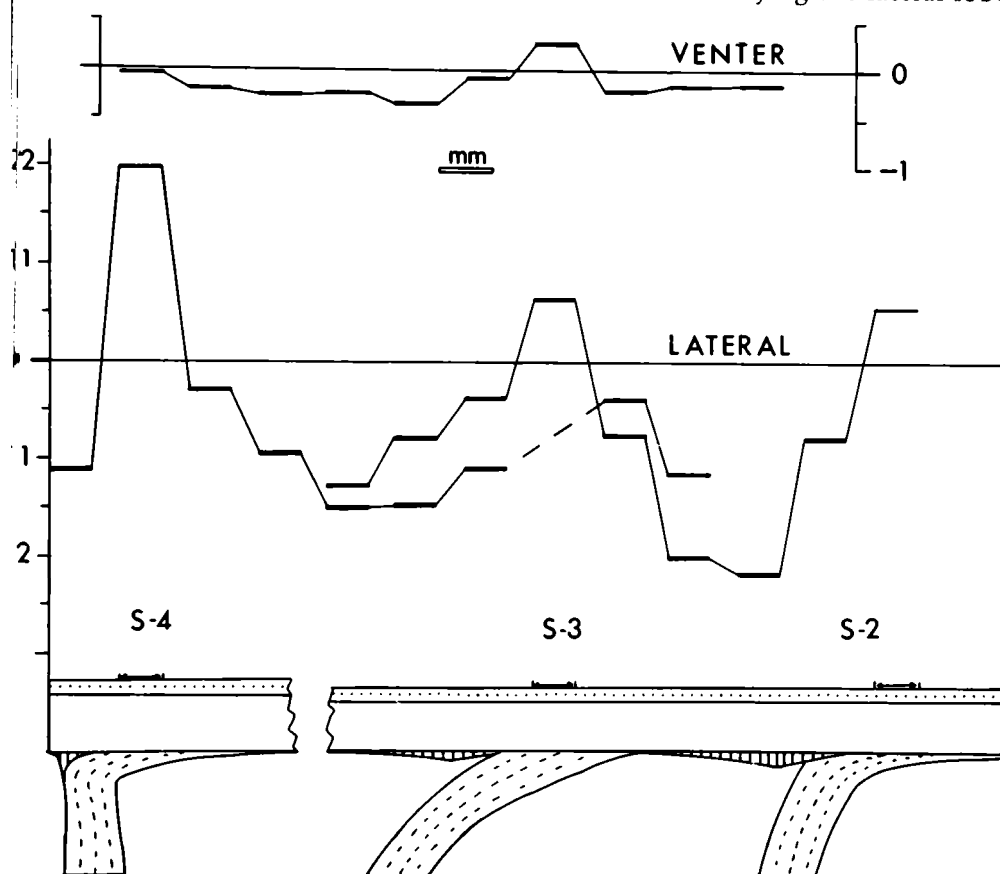


Fig. 3. Strain variation in the outer layer of the *Nautilus* shell wall, due to bending stresses related to the position of the septal sutures and compressive membrane stresses (see Fig. 2 for positions of the three series of strain gauges). These results imply that the ventral shell wall is very strong and transmitted little circumferential stress to the hemispherical region of the septa. In contrast, the sutures of the lateral lobe caused tensile bending stresses over the sutures and compressive bending stresses between the sutures (indicative of tension internally), that were large enough to risk the failure of the relatively weak outer shell layer. (Divide units of strain shown here by 1×10^4 to obtain the strain ϵ at 0.685 MPa, proportional to pressure). Accurate sections obtained by subsequent sectioning in the plane of the EA-06-030TY-120 gauges (and strain measurements) show that the strain varies due to the angle of incidence of the septal sutures (below), as well as the angle between the gauges and the principle compressive strain axis of the shell wall (Fig. 2). Tensile strains are increased by the compressive hoop stress resultant in the S-3 to S-4 series, and directly reduced by the compressive hoop and axial stress resultant in the S-3 to S-2 series. This will be discussed elsewhere.

pillar-flute (Fig. 2) is influenced by bending stresses that are large enough to fracture the outer shell wall at a depth similar to that of the implosion of the last septum (Fig. 3).

PFAFF (1911: 221) outlined so-called laws of sutural differentiation ("Gesetze der Lobendifferenzierung"), which are the source of the view that the length of the ammonitic suture should increase as the square of the linear dimensions, when suture thickness and hydrostatic pressure are constants (WESTERMANN 1971: 20–21). The hydrostatic load or force applied normal to the last septum at a particular depth was proportional to the inner cross sectional area of the whorl. It is doubtful whether it was more than 1 MN in the largest or more deep-water ammonoids. PFAFF (1911) postulated that shear stress was generated along the suture; presumably by the inward movement relative to the adapically contracting and circumferentially compressed shell wall. This shear stress would not be related to the cross sectional area of particular flutes on the septum, and it may be doubted whether it was as important as membrane and bending stresses. It is curious that efficacious anti-shearing adaptations such as the internal mural ridge (Fig. 3) and transverse ornaments of nautiloids, were replaced by a planar surface of lobe attachment analogous to lapped joints. But, since the load is largely transferred at the ends of lapped joints (GORDON 1978: 137), there was little advantage in increasing suture width.

The complex nature of the bending and shear discontinuity stresses at the suture of pressure vessels (ROARK 1954: 264–267), and size-related increases in bending stresses, further complicate the "PFAFF model". According to COWAN (1976: 280) the membrane stress in anticlastically curved, "hyperbolic paraboloids" generates internal catenary shear forces aligned at 45° to the flute axes. The constant membrane shear stress (SALVADORI 1971: 283) can be estimated from an equation which assumes that the flutes are supported by tensile stresses in the shell wall (SALVADORI 1971: 280). It is described as being "deceptively simple" due to the magnitude of additional bending stresses generated in highly fluted, ammonoid-like surfaces (COWAN 1976: 282). It will be noted that both flute amplitude and septum thickness strengthen the last septum when the bending stresses are not too large:

$$\sigma = P \quad K/A \quad d_s$$

where: σ = membrane shear stress in MPa

P = hydrostatic pressure in MPa

K = cross-sectional area of septum in m^2

d_s = septum thickness in m

A = flute amplitude in m

2.2 Membrane stresses in the last septum

The ammonoid septum is a surface of anticlastically curved arcs or saddles; termed saddle-flutes to reduce confusion between the engineering term saddles and the concave-out transverse arcs of these saddles, termed

saddles in palaeontology. The saddle-flutes developed orthogonal tensile and compressive membrane stresses, in addition to large bending stresses due to pressure applied via the body chamber. There are also circumferential compressive and bending stresses, of about half the magnitude applied to internal septa. The saddle-flutes of Cretaceous *Leymeriella tardefurcata*

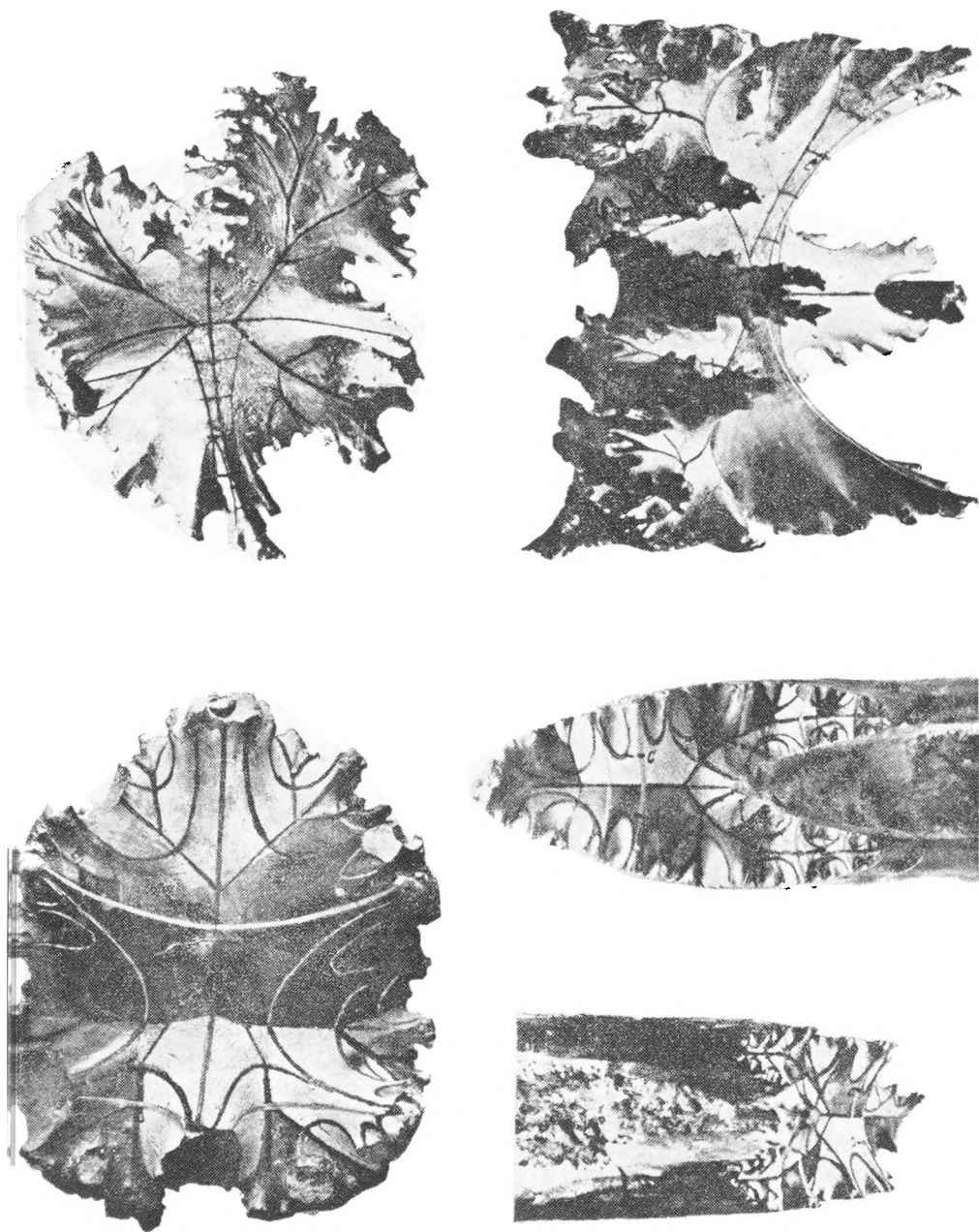


Fig. 4. Reproduction of Plate 11 of PFAFF (1911), showing the saddle-flute axes (R_1 curvature) of the septum of *Leymeriella tardefurcata* and (1 a, b) the saddle-flutes of *Crioceras* and *Dorsetensia* (2-3). Plaster replicas of the specimens (lacking the lines drawn by PFAFF) were studied at McMaster University.

(LEYMERIE) and two other Mesozoic ammonoids are illustrated by our reproduction of the original plate 11 of PFAFF (1911) as Fig. 4. The lines drawn on the *Leymeriella* septum are axes of the marginally bifurcating saddle-flutes that display their large radius of curvature R_1 on Fig. 4 b. The smaller and more variable curvature radius R_2 is in a plane normal to each of these curved axes. The additional lines drawn on the other two septa are the "stress lines of the principle and subsidiary vaults" of PFAFF and have no significance in the modern interpretation. Their "characteristic points" (c) and the implication that the R_1 is a catenary curve which transferred stress to the shell wall, are questionable concepts.

Since the stresses in saddles cannot be calculated (G. AE. ORAVAS in WESTERMANN 1975: 245; COWAN 1976: 282), it is helpful to discuss membrane stresses in synclastically curved figures of revolution (ROARK 1954: 269), such as the shell wall of an ammonoid, in which the orthogonal stresses are entirely compressional or tensional at one point on the surface. The preference for saddles in architecture is due to the possibility of constructing two saddle designs from straight lines (COWAN 1976: 280). The apparent advantages of a synclastic convex-out curvature in ammonoid septa designed for the "PFAFF model", were lost due to the greater bending moments developed under circumferential pressure and constructional difficulties. The membrane stresses in a synclastically curved septum are as follows (provided that R_2/d_s is more than 10 and less than infinity):

Hoop (maximum) stress $\sigma_1 = P R_2/2d_s (2-R_2/R_1)$

Axial stress $\sigma_2 = P R_2/2d_s$

Where: σ = membrane stress in MPa (MN/m²)

P = hydrostatic pressure in MPa

d_s = septum thickness (like P measured normal to surface) in same units as R

R_1 = axial radius of curvature of membrane

R_2 = transverse radius of curvature

If these equations were applicable to ammonoid saddles they indicate that the maximum R_2/R_1 ratio of 0.5 increased the implosion depth by one and a third relative to a cylindrical pillar-flute with the same length and (shell) thickness. The increase in axial length and weight due to curvature would neutralize this increase in strength in a minimum weight structure. The circular axial curvature (R_1) and average convex-out morphology of the ammonoid septa (SWINNERTON & TRUEMAN 1918: 32), is less critical than the development of a large tensile hoop stress due to flattening of the transverse sections of the saddles. Thus the goniatitic-Z and goniatitic-M sutural types of WESTERMANN (1957 a: 241) seem poorly adapted in terms of the "PFAFF-model".

This view is refuted by a comparison of *Goniatites choctawensis* SHUMARD (CM 176) with a "*Phylloceras plasticum* BURKHARDT (J2119) from Cualac in Mexico. At the 19 mm conch diameter growth stage the siphuncle strength index of the *Goniatites* was slightly greater than an "adult" *Nautilus* (radius 330 μ m, thickness 45 μ m) and the circular arcs of the saddle-flutes had a R_2/d_s ratio of 18 (1.2 mm/0.07 mm) away from the sutural zone where the stress cannot be discussed using the above formula. The largest of the internally similar umbilical saddle-flutes in the 90 mm diameter *Phyllo-*

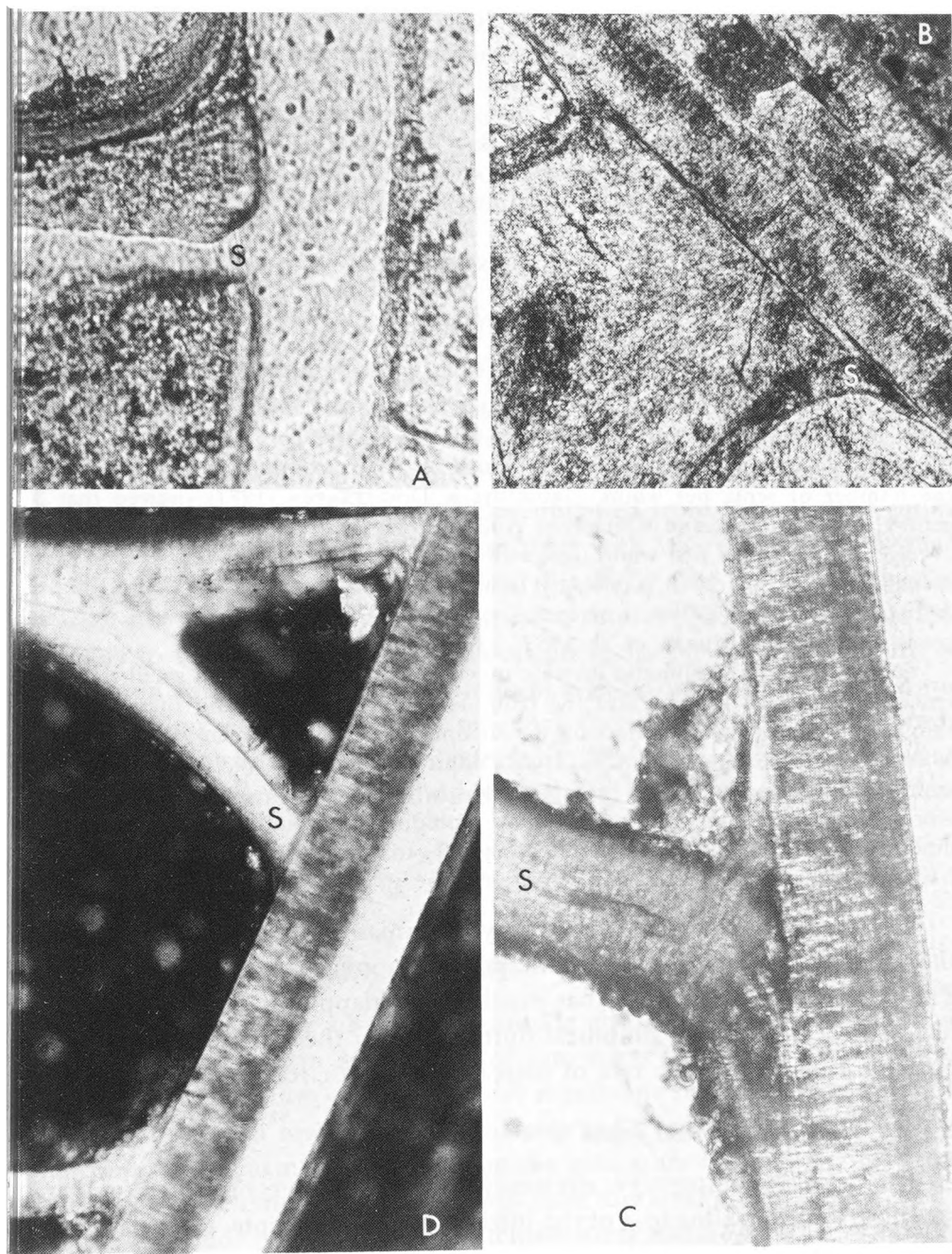


Fig. 5. Thin sections of *Goniatites* (CM 176) and *Haplophylloceras* (J20341) illustrating the sutures seen in transverse sections of the phragmocone. A. Phosphatic connecting ring and adjacent sutures of *Goniatites*, x 415. B. Same specimen showing mural ridges behind the septa, x 140. C. Mural ridge supporting the internal edge of foliole in *Haplophylloceras* x 380. The septum (below) slopes towards the adjacent connecting ring situated beyond the right margin of the photograph. D. The narrower, more orthogonal and mural-ridge-free sutures of the adjacent lobule in the same section, x 165 (also note the relative thickness of the white outer prismatic layer and dark nacreous layer, seen in the overlying ventral shell wall). S = septum. See also Fig. 8.

ceras had a slightly greater R_2/d_s ratio of 20 (3.5 mm/0.18 mm). The greater thickness of the *Haplophylloceras* septum (J2034L) compared to a *Goniatites* septum supporting the same 0.125 mm thickness of shell wall (Fig. 5) is presumably related to bending stresses in the longer flutes. The large *Pachydiscus* septum (Ammonitina) described by WESTERMANN (1975: 246) shows a reduction of R_2/d_s from 20: 1 in the middle of the septum to 4: 1 within 1.5 mm of the shell wall. If the *Goniatites* had a similar habitat depth as the above *Phylloceras*, then the membrane stresses in their last septa were of comparable magnitude.

The gross morphology of sutures is predicted from membrane stress theory. The alignment of the flute axial traces normal to the adjacent umbilical shell walls and along the shortest distances across the ventral septum, permitted the constant radius R_1 to attain a minimum value. R_2 cannot be greatly increased relative to R_1 and d_s is inverse to septal spacing (in radians) in a minimum weight structure. The outward expansion of R_2 in each umbilical saddle-flute is proportional to the increase in whorl circumference per whorl and critical to their strength. The variation in septum thickness (d_s) in these flutes potentially varied by a factor of two, due to the range in the number of septa per whorl. DRUSCHITS & DOGUZHAIEVA (1981) showed that 31 genera of late Jurassic and Cretaceous Ammonitina, Lytoceratina and Phylloceratina average 12.8 septa per first whorl (range 10–17) and show a greater variation of septal spacing in ontogeny than phylogeny (range 10–22). *Goniatites* and Lower Jurassic Ammonitina contain as few as 5 septa per whorl; but the average is similar to Cretaceous ammonoids (MILLER et al. 1957: L16, DOGUZHAIEVA 1982).

Septum thickness could also increase in whorl cross-sections with a small circumference (X) to square-root-of area (K) ratio. This ratio decreased and then increased through ontogeny; but the effect on d_s was only significant between widely different whorls, such as orthocones (3.55: 1) or "adult" *Dactylioceras* (4.09: 1), the typical ammonoid ratio, and highly compressed *Radstockiceras involutum aequidellatum* GÉCZY (7.25: 1). Thus the most involute ammonoids, with the largest number of umbilical flutes and the greatest tendency for R_2 to enlarge along the flute axis, may have also had to reduce d_s due to an increase in shell density.

It is suggested that the morphology of goniatitic septa is consistent with the function of resisting hydrostatic pressure applied via the body chamber. This "PFAFF model" predicts that involute (overlapping) whorls will tend to have a larger number of umbilical flutes, and that their number will increase both with depth and the rate of increase in whorl circumference per whorl.

2.3 Buckling of internal septa

The critical compressive stresses for general Euler buckling (σ_E) and marginal local buckling (σ_L) of the internal ammonoid septa, must have been larger than the maximum local compressive stress normally applied to them in the "WESTERMANN model" (1975). They are a function of shell stiffness (E , WAINWRIGHT et al. 1976: 249–252) and are only one of a number of parameters limiting shell strength in compression.

$$\sigma_L = \frac{k E t}{2 R_2} \quad \sigma_E = \frac{n \pi^2 E}{(L/r)^2}$$

Where E = YOUNG's Modulus in MPa (4.7×10^4)
 k = constant often taken as 0.65

- R_2 = minimum curvature radius of flute in m
- n = constant of 4: for rigid suture (probably less)
- L = linear axial length of flute in m
- t = septum thickness in m, measured parallel to shell wall
- r = least radius of gyration. It cannot be calculated due to the complexity of the ammonitic sutures and their variation along L ; but approximates to $0.6 R_2$ for a cylindrical flute.

Buckling equations explain the tendency for the "*Phylloceras*" *plasticum* (J2119) to have a flat septum surface aligned within the plane of the hoop stress in each whorl. If the flutes were cylindrical elements aligned normal to the pressure within this plane (pillar-flutes), they would not have buckled in the middle until their crushing strength was exceeded by a factor of 80 (33 GPa). Saddle-flutes developed bending stresses due to their initial axial curvature (BAYER 1977a: 360) and buckled at much lower pressures. The measured R_2/t ratio of $550 \mu\text{m}/40 \mu\text{m}$ obtained from the phylloid suture implies that σ_L was < 1350 MPa. Since septa with a R_2/t ratio of more than 50 probably failed by elastic instability, it is likely that the rather constant average curvature and minimum thickness at sutures (WESTERMANN 1971: 21), was due to limitations imposed by local buckling. The minimum width of the septum approached the critical ratio of R_2/t in order to increase r in the Euler buckling equation; but the tendency for the suture to be uniformly distributed over the shell wall decreased r . The flute orientation reduced their "slenderness ratio" by minimising L and seems consistent with the "WESTERMANN model".

2.4 Bending stresses in the shell wall

Bending stresses are of equal magnitude and opposite sign at the same distance from a median neutral axis of zero stress situated in the septa and shell wall. The addition of a compressive membrane stress results in a shift in the zero stress layer towards convex margins and a consequent subtraction of the compressive membrane stress from the maximum tensile bending stress. Similarly a tensile membrane stress will shift this layer towards the concave margin. It is added to the maximum tensile stress at the convex margin. The ultimate compressive stress is at least double the ultimate tensile stress in *Nautilus* nacre and four times the ultimate tensile stress in the outer layer of the shell wall. It is advantageous to add compressive membrane stresses to tensile surfaces produced by the bending of the shell wall over sutures. But the addition of the tensile membrane stresses resulting from the concave-out curvature of the last septum, to tensile bending stresses generated on their internal surface under circumferential compression, will greatly reduce the septum implosion depth. It is also important to avoid the development of a large bending moment at the suture.

In the simple case of a flat square of shell wall simply supported on a rectangular suture grid, the maximum central bending stress is given by PRESCOTT in ROARK (1954: 203):

$$\sigma_{\max} = 0.22 P (e/d_w)^2$$

where $\sigma_{\max}$ = maximum bending stress in MPa

P = pressure in MPa

e = minimum suture spacing along square in m

d_w = shell wall thickness in m

This equation implies that e/d_w is an insensitive depth index below a depth of about 300 m (Fig. 6). If the tensile strength was only 100 MPa, then the variation of e/d_w from 12:1 in a 15 mm diameter oppeliid, to 8:1 in a 40 mm diameter oppeliid, implies a depth increase from 300 m to 750 m in ontogeny (nearly flat whorls from Chile locality 1-200781 GCH). The flanks ($R_2 < 150$ mm) of a 0.2 m diameter (*Calliphyllloceras* (J1828) had no unsupported whorl areas with e more than 5 mm. The shell thickness of about 1 mm implies that a tensile bending stress of 100 MPa would have occurred at a depth of 2000 m. This is over twice that deduced from the connecting ring (WESTERMANN 1971: 26).

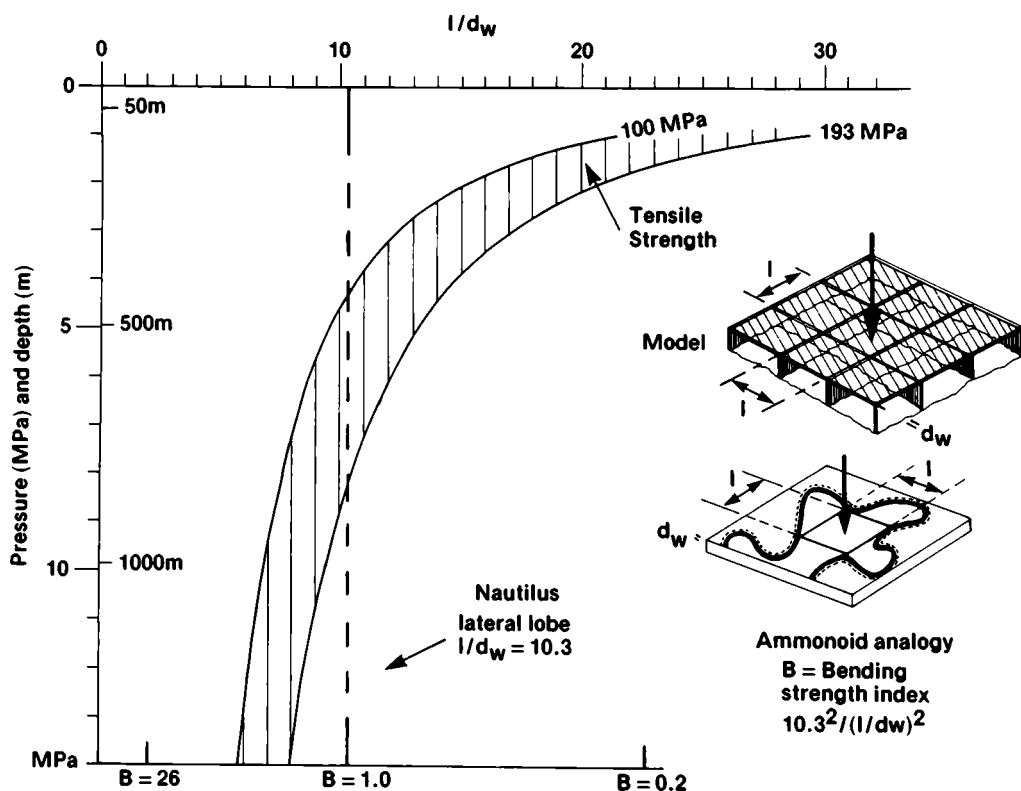


Fig. 6. Model illustrating the tensile bending stresses generated within a flat sheet, supported by a rectangular grid against an external hydrostatic pressure. The application of this model to the illustrated situation involving the largest unsupported squares on flat ammonoid whorls, implies that complexity of ammonitic sutures is unlikely to be a very sensitive depth index (although it could of course be correlated to depth through some other function of these sutures).

Real sutures presumably developed larger bending stresses than a rectangular grid and like the grid developed a slightly higher stress over the sutures than between them. But these external tensile stresses were reduced by membrane stress. The suture of an 10 mm diameter *Calliphyllloceras* (J1826, HALL & WESTERMANN 1980: 62) had a lateral density (Y/S) of 0.71 mm/mm^2 and a thickness of $115 \text{ }\mu\text{m}$ ($R_2 = 100 \text{ mm}$, $d_w < 0.9 \text{ mm}$). The pressure was concentrated by a factor of 12 within these marginal septal supports. The distance e was 2.7 mm in the lateral saddle, and 4.3 mm in the lateral lobe (Fig. 6). These calculations are consistent with the "WESTERMANN model" in which the bending stresses in the shell wall were more critical than the circumferential stress applied per unit area of suture.

The buckling failure of an ammonoid shell only required the development of a tensile bending stress of up to 115 MPa in the outer shell wall, due to inadequate stiffness (E) for a given whorl shape. According to CURREY (1977) the brittle nacreous shell of *Pinctada* deformed elastically to a stress of about 100 MPa and a strain of 0.002 , although it did not break until a stress of over 200 MPa and a combined plastic and elastic strain of 0.011 (stress as Modulus of Rupture in bending tests). The ammonoids would have failed at the elastic limit (yield point) at an axial strain of < 0.003 (Fig. 3).

2.5 Bending and discontinuity stresses in septa

The ventral hemispherical part of the last *Nautilus* septum is analogous to pressure vessels, in which the discontinuity stress generated by differences in the hoop strain of the spherical septa and cylindrical shell wall, does not produce bending stresses at the suture. There are likely to be small bending moments on either side of the suture; but they are much smaller than the bending stresses generated normal to the hoop stress in sutures with an angle of 45° or more in this plane (FLÜGGE 1973: 348–351). These high angles are, however, required in the lateral lobe of *Nautilus*, where the flat shell wall needs internal support against circumferential pressure. In this region the orthogonal sutures only occur in the axial region of a cylindrical pillar flute and are aligned within the plane of the shell wall hoop stress (Figs. 2 and 3).

The discontinuity stress at the *Nautilus* suture is related to the difference in membrane strain between the semi-circular pillar-flute axis with a marginal R_2/d_s ratio of $14:1$ ($20:1$ in mid-septum) and the transverse whorl section with a R_2/d_w ratio of 250 to $100:1$. An 0.9 mm wide orthogonal suture (Fig. 3) showed that the neutral axis of the septum is inclined at 20° to the shell wall within 0.5 mm of the suture. This sharply bent concave-out margin of the septum is buttressed by the mural ridge. The tensile strain in the outer shell layer peaks over the suture of the median neutral axis and abruptly changes to compression over the mural ridge (Fig. 4). The marginal sutures of this internal pillar-flute have twice the length of the axial zone and their concave-out septa are inclined at 30 to 60° , with a suture angle of about 20° at the neutral axis.

The geometry of the marginal septum (Figs. 5–8) has been given little attention during discussions of ammonoid functional morphology, and has been explained by constructional processes (WESTERMANN 1975: 248–250). The similar design of sutures has been obscured by one spurious (WESTERMANN 1972) and one real case of Cretaceous ammonoids with inverted suture lines (WESTERMANN 1975: 249). The heteromorph *Glyptoxoceras* does not disprove the proposition that there was a selection pressure favouring the design of sutures with a convex-out subcircular arc flanked by "tiepoints" (SEILACHER 1975).

Convex-out arcs are particularly developed in phylloid sutures evolved independently in adventitiously added saddles of the Permian *Cyclolobidae* and *Perrinitidae* (MILLER et al. 1957: L21); or the Triassic *Megaphyllitidae* (WIEDMANN 1972; VAVILOV 1978) and Jurassic-Cretaceous *Phylloceratina* (WIEDMANN & KULLMANN 1981), which added pairs of saddles near the umbilicus. If it is safe to generalise from a 34 mm diameter *Haplophylloceras* (J2034L), then it appears that the "tie-points" result from the projection of the 135 μm thick and tightly curved axial surface ($R_2 = 0.2$ mm) of lobules at about 20° to the shell wall; while the rounded folioles display a circular curvature ($R_2 = 0.5$ mm) of nearly constant thickness 75 μm , projected at 45° until close to the inner edge of the suture. The transverse angle of contact varies from more than 75° over two thirds of the 70 μm thick lateral region of the lobules ($R_2 > 0.8$ mm) to 45° across the sub-triangular "tie-points". The outer 45 % of the shell wall (d_w) consists of a relatively weak prismatic layer. Since it would have been in tension over

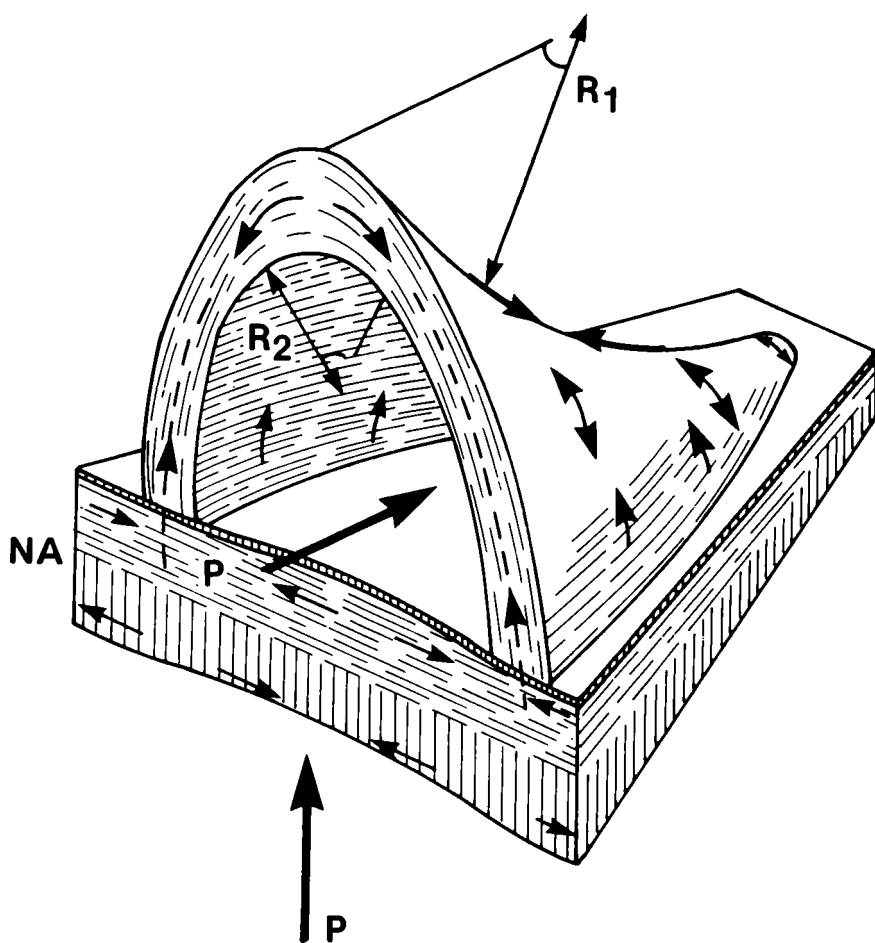


Fig. 7. Diagram illustrating the likely stresses within a lobule of the last septum of an ammonoid, just after the removal of cameral liquid from the final, completed gas chamber. The diagram, based on the *Haplophylloceras* section of Fig. 5, shows the large axial radius of curvature of the lobule (R_1), the variable transverse radius (R_2), the increase in septum thickness developed to avoid the bending of the lobule axis under the circumferential load (P) and the related bending of the neutral axis (NA) of the shell wall. The horizontal arrow (P) illustrates the hydrostatic pressure acting directly on the surfaces of the lobule (via body chamber) that develops tensile membrane stresses within the transverse arcs with concave-out curvature.

the sutures the bending moments in the shell wall cannot have been large (Fig. 7). *Spirula* has an entirely prismatic shell wall (Fig. 8 C).

Due to the anticlastic curvature of ammonoid septa, it is questionable whether the discontinuity stresses in the nautiloid hemispherical septa explain the axial orientation of the low-angle parts of goniatitic sutures, or the largely random orientation of lobule axial trends in complex ammonitic sutures. Both ammonitic and goniatitic sutures had slightly expanded orthogonal sutural junctions along the long margins of their lobes and lobules, with a high-angle sutural contact of the median neutral axis (Fig. 5 A, D). In contrast, a longitudinal section through a *Haplophylloceras* foliole shows a *Nautilus*-like suture complete with mural ridge (Fig. 5 C). The low-angle junctions of the lobes and lobules (Fig. 8 A-B) increased the curvature and area of the convex-out arcs of the last septum. The stresses related to R_1/d ,

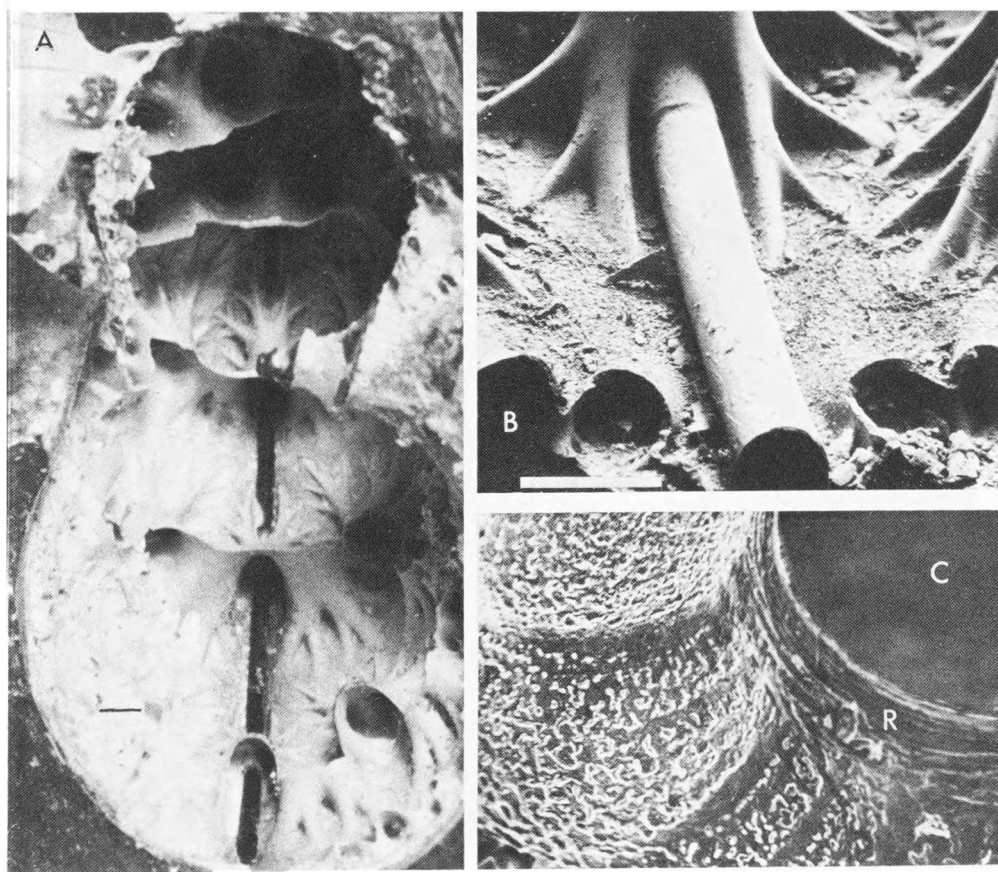


Fig. 8. Examples of anticlastic curvature. A. Anterior view of the chambers of *Haplophylloceras* (J2034, x 6, bar = 1 mm). B. Posterior view of the lobules sectioned on Fig. 5 C-D (x 21, bar = 1 mm). C. Lateral external view of chambers 5 to 7 of a *Spirula* (Discovery Sta. 6689) showing a ridge of axial aragonite fibres (R) along the anticlastically curved whorl surface (x 64).

were compressional and the more dangerous orthogonal tensile hoop stresses were reduced by the centrifugal decrease in R_2/d_s . In addition, the tensile membrane stresses in the concave-out transverse arcs of the lobules, were reduced by compressional membrane stresses near the suture. The greatly reduced R_2/d_s ratio of 1.5 in the axial zone of the *Haplophylloceras* lobules, served to reduce bending stresses resulting from the large distance between the compressional axis of the flute and the compressional load applied via the lobules (Fig. 7).

The convex-out curvature of saddles and folioles resulted from the need to avoid tensile σ_1 and σ_2 membrane stresses, in a region of the last septum developing tensile bending stresses. The compressive σ_2 membrane stress helped to reduce tensile bending stresses in the saddles of the last septum; but they cannot have been large or the structure would have later collapsed. The constructional control of foliole morphology implied by ARKELL (1957 a: 243) and later authors cannot be accepted here. The increase in the frequency of linear foliole elements in the complex ammonitic sutures of the *Lytoceratina* and *Ammonitina*, may have resulted from an alternative reduction of circumferential stresses; but need not apply a reduction in the implosion depth of the last septum. These sutures show a more equal and higher density of coverage of the whorl section than phylloid sutures, suggesting a reduced r and circumferential load within saddle-flutes.

Lytoceratina such as Cretaceous *Pseudophyllites* added an internal convex-out bulge to the septum. Their "dorsal tunnel" (septal lobe) has a rather flat termination that is supported by the previous bulge at the point of maximum concavity, so as to act as a whorl and septum within a whorl. It presumably reduced bending moments and R_1 in the radial flutes of this evolute conch, as adaptations to the "PFAFF model".

2.6 Statically indeterminate stresses

The statics of septa implied by the "PFAFF model" restricted the morphology of goniatitic and ammonitic sutures. In addition the increased length of ammonitic sutures reduced the circumferential stress in thin marginal septa, adapted to decrease bending stresses resulting from ontogenetic increase in the maximum suture spacing/shell wall thickness ratio. The probable redundancy of some sutural supports indicates that these bending stresses are statically indeterminate, like a simply supported beam on three supports (DEN HARTOG 1949: 95). They also become statically indeterminate by ascent in the water column, and by the later overgrowth of internal sutures. In order to reduce the unwanted force X in redundant suture elements ($X = 5/8 P$ of a beam, DEN HARTOG 1949: 94), it was advantageous for sutures to be analogous to a spring supporting a relatively rigid shell wall. Thus if the frilled margin of the septa acted as "springs" then the force X is greatly reduced by a small increase in the flexibility (decrease in rigidity) of the marginal septal supports (DEN HARTOG 1949: 96):

$$X = (5/8 P e)/1 + (K_w/K_s)$$

where X = redundant upward force in MN

P = pressure on whorl in MPa

e = suture spacing along hypothetical beam element of wall in m

K_w = spring stiffness of wall

K_s = spring stiffness of marginal septal supports

Analogies between this situation and the thin saddle-flutes on the ventral margin of *Sepia* intracameral walls (Fig. 9) and ammonitic sutures (Fig. 8A-B), suggest that it was advantageous to introduce flexibility into compressional support elements of thin shells. Ammonitic sutures and the outer prismatic layer may have also served as shock absorbers, for reducing the damage resulting from impact point stresses. The surprising flexibility and

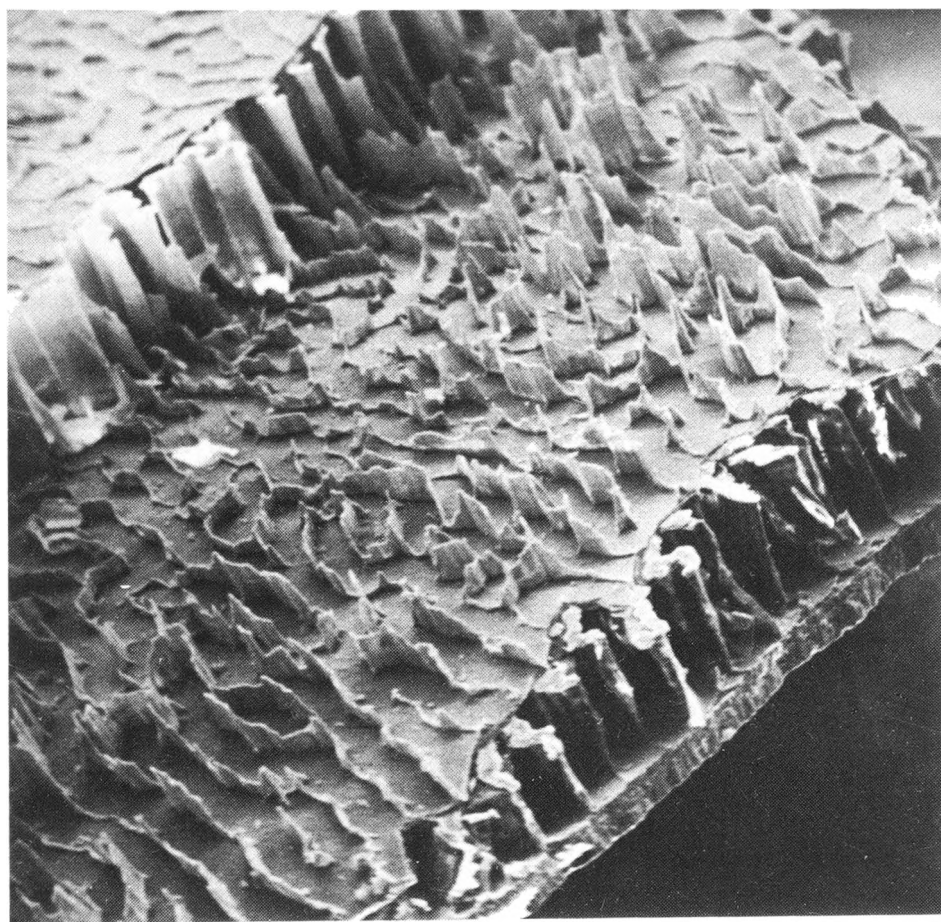


Fig. 9. Ventro-lateral view of a fractured chamber of a juvenile *Sepia officinalis* L. (reared at Naples by A. PACKARD) showing the radial intracameral walls which support the thin planar septa. Dorsal shield seen below. Although the walls are pillar-flutes under a ventrally imposed hydrostatic load, it will be noted that they approach the anticlastically curved and corrugated morphology of an ammonoid septum near the ventral side of each chamber (x 40).

durability of the thin, prismatic *Argonauta* shell (OWEN 1839), is related to the moisture content and other properties of organic components situated between the prisms and along a subcentral spherulitic membrane (Fig. 10).

2.7 Testing hydrostatic interpretations

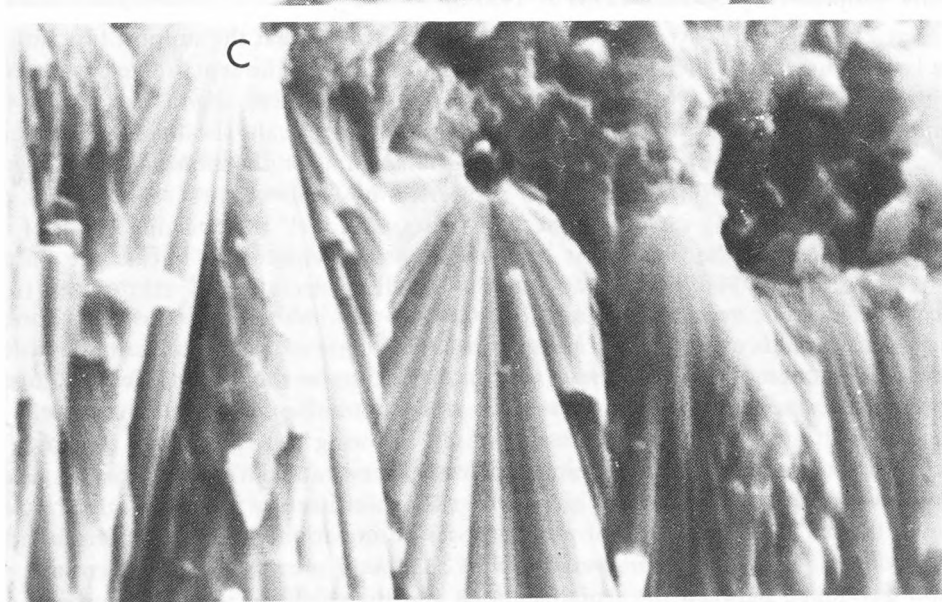
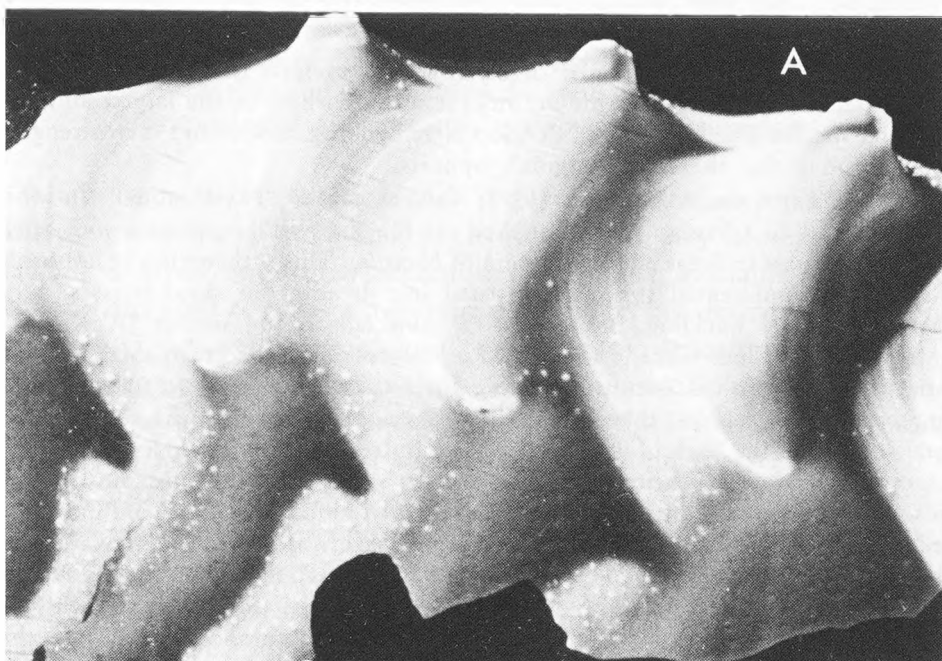
One test of these interpretations would be strain measurements on metal models of appropriate stiffness and Poisson's Ratio. An experiment with plastic models of nautiloid and goniatite-like fluted septa, employed constant differential air pressure to simulate the strain in the internal and last septa of phragmocones. The axial strain in the middle of a lobe spanning a cylinder with a cross-sectional ratio of 2:1, increased from a moderate tensile strain internally to a large compressive bending strain in the last septum. The internal tensile strain was approximately equal to the compressive bending strain within the model nautiloid septum supporting the same type of cylinder. The maximum external compressive strain between the simple concave septa and the axial surface of the u-shaped goniatitic lobes had a similar magnitude; but the latter displayed more asymmetry culminating in a tensile strain of three times the maximum compressive strain. It occurred near the unsupported u-shaped "tie-point" and might be reduced at the edges of the more flexible, thin septa in the saddles and tapering lobes of real ammonoids.

In addition to *Nautilus*, the coleoids *Spirula*, *Sepia* and *Argonauta* have shells which give an insight into ammonoid shell functions. *Spirula* is an internal, open-planispiral to torticonic phragmocone, adapted to great depth. *Argonauta* is an external planispiral shell, with no septa and very rapidly expanding whorls adapted for flexibility (OWEN 1839). *Sepia* has an internal shell, with fluted internal walls and thin flat septa, adapted to resist crushing pressure.

The "test" suggested here is to describe the morphology and phylogeny of ammonoids using concepts related to their functional morphology. There appear to be two alternative mechanical models for the hydrostatic function of septal sutures. Each model is divided into several potential hypotheses concerning the way in which the suture functioned within the model:

1a) The original "PFAFF model" (1911) assumed that the last ammonoid septum was supported against hydrostatic pressure by transfer of stress to a strong shell wall (Fig. 4). This is unlikely to be true and his precise predictions from the model are therefore of

Fig. 10. Vento-lateral view of the fractured exterior of the ammonoid-like, spherulitic calcite shell of *Argonauta hians* SOLANDER (Discovery Sta. 6689). A. x 11 showing ventral "hydrofoils" and ribbing. B. External pustules and subcentral membrane (bar scale = 40 μm). C. Calcite prisms radiating from sites within the subcentral membrane (bar scale = 4 μm).



questionable value. It is certainly inconsistent with his discussion of membrane stress in septa.

1b) A provisional "PFAFF model" is based on the premise that the largest area of sutural attachment occurred in the strongest arcs of whorl of the largest and most deepwater species. The septa would develop large bending stresses and their strength is analogous to a flat sheet on marginal supports.

1c) The SAUNDERS & WEHMAN (1977) version of the "PFAFF model", in which circumferential compressive stresses applied via the shell wall, combined with tensile membrane stresses to break the last septum of *Nautilus*. This is theoretically impossible unless the circumferential stress is translated into bending or shear stresses, as for example in Euler buckling. BAYER (1977a) objected to the similar "WESTERMANN model" on the grounds that the ammonoid septa were likely to convert small circumferential stresses into disastrous bending stresses. In other words their critical compressive stress was less than circumferential stresses applied via the shell wall and septal sutures. In the "hybrid PFAFF model" the fluted morphology of septum evolved to locally increase the rigidity of the last septum subjected to unfortunate combinations of tensile bending and membrane stresses. It would involve a general increase in shell wall strength, which reduced circumferential loads applied to particularly weak parts of the septum (Fig. 7). The "hybrid PFAFF model" is similar to the RAUP & TAKAHASHI (1966) interpretation of *Nautilus* septa and is consistent with the dominance of membrane stresses in the central regions of ammonoid septa below their critical Euler load (σ_E).

1d) The statically indeterminate "hybrid PFAFF model" in which the shell wall locally developed tensile membrane stresses and strains, due to outward concavity. Thus the supporting shell wall would be locally stretched and locally contracted over the suture. Sutural complexity increased to reduce the statically indeterminate stresses resulting from local occurrences of tensile circumferential stress in the last septum. The ornamentation, umbilical morphology and heteromorphism seen in Mesozoic ammonoids can therefore be linked to their increased sutural complexity. But as in all "hybrid PFAFF models" the strongest and most complex ammonitic sutures would occur under the weakest shell wall arcs of the most deep-water species (Fig. 6). This version of the "PFAFF model" is the closest acceptable approach to the tensile loading model of suture proposed by ARKELL (1957a, 1957b).

2a) The original "WESTERMANN model" (1975) assumed that the support function of the last septum in the "hybrid PFAFF model" increased until the septa served as internal struts for supporting a weak-shelled conch. Thus the crushing depth implied by the compressive membrane stresses in the unsupported shell wall should not be significantly greater than the implosion depth of the septum, or the rupture depth of the siphuncle (Fig. 2-3). This model was supported by WAINWRIGHT et al. (1976).

2b) In the buckling version of the "WESTERMANN model" the crushing depth of the shell wall exceeded the equivalent compressive stress required to buckle the unsupported shell wall. Failure by local tensile bending stress could also result from predation by some vertebrates. Uncoiled heteromorphs, multi-whorled evolute conchs and streamlined oxycones should therefore have stronger septal supports than involute *Nautilus*. HENDERSON (1984) appears to regard buckling as the only mode of failure in compression and attempted to reject this version of the "Westermann model", by analogy with steel cylindrical pressure vessels showing a larger plastic strains.

2c) In the statically indeterminate "WESTERMANN model" the ammonitic suture evolved as a support structure of the septum which efficiently increased safety factors during the random application of point stresses during accidents or predation. It aided the evolution of intra-specific variations in shell wall morphology and reduced the stress developed between the septal supports and the shell wall during upward migra-

tions of the type observed in *Nautilus* by WARD et al. (1984). The experiments of CHAMBERLAIN et al. (1983) were conducted in a way that did not realistically simulate the effects of this version of the "WESTERMANN model". The known axial compression of the lateral lobe surface and the overlying shell wall (Fig. 3) indicates that the "PFAFF model" is only valid within the ventral, quasi-hemispherical region of *Nautilus*.

Many aspects of these models represent extremely interesting and difficult problems of structural mechanics, which may be solved by finite element analysis and other techniques becoming available to engineers. Work of this kind requires a new type of accurate and descriptive palaeontological data, as well as geological estimates of depositional depth. The generally complete preservation of the septa and siphuncle in offshore ammonoid assemblages is inconsistent with the "provisional PFAFF model", the RAUP & TAKAHASHI (1966) version of the "hybrid PFAFF model", and the epipelagic habitat suggested by HENDERSON (1984). The strains produced by predatory vertebrates provide evidence about the strength and stiffness of the shell wall at high strain rates, which gives little support for the buckling version of the "WESTERMANN model". Thus the simple compressive stress in the shell wall at the implosion depth, is the main mechanical criterion determining the relative importance of models 1 d and 2 c.

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