Is cephalopod septal strength index an index of cephalopod septal strength?

JOHN A. CHAMBERLAIN, JR AND REBECCA B. CHAMBERLAIN

THE BATHYMETRY of fossil cephalopods has been a singular irritant to students of these animals for many years. On the one hand, living depth is recognized as a key parameter in reconstructing cephalopod palaeoecology, but on the other, quantitative techniques for establishing palaeobathymetry have been notoriously elusive. A solution to this quandary seemed apparent as a result of two discoveries made about 15 years ago: 1. hydrostatic pressure greatly exceeds cameral gas pressure in Nautilus, and 2. the maximum pressure simple septa can withstand may be related to septal geometry.

The former of these ideas is by no means new (e.g. Pfaff, 1911), but no firm substantiation for it existed until the work of Bidder (1962) and Denton & Gilpin-Brown (1966). In puncturing fresh shells which had been immersed in liquid paraffin, these authors noted that no gas bubbles escaped as would have occurred if gas pressure inside the shell exceeded atmospheric pressure. In Nautilus, therefore, cameral gas pressure is about 1 bar whereas ambient hydrostatic pressure reaches markedly higher values, of the order of 20-40 bars at the modal depth of Nautilus. The imbalance between internal and external pressure elicits a pressure gradient across the phragmocone which must be resisted by the strength of the shell. Denton & Gilpin-Brown (1966) imploded three specimens of N. macromphalus, and found failure to occur at pressures of about 70 bars.

These results led to a series of papers reporting experimental determinations of shell strength using empty shells (Raup & Takahashi, 1967; Saunders & Wehman, 1977) as well as live animals (Ward & Martin, 1980; Ward et al., 1980; Kanie et al., 1980). The main outcome of these efforts has been to show that maximum shell strength is in the region of 75-80 bars) for N. macromphalus, and perhaps slightly higher for Fijian N. pompilius. Nautilus cannot therefore survive at depths greater than about 800 m.
The mechanical properties of the load-bearing elements of the shell — the shell itself plus the septa and siphuncular tube — are clearly factors of paramount adaptive value. The fundamental unity in bauplan among virtually all eoctocochliates implies that most fossil cephalopods also maintained low cameral pressures, and like Nautilus were subject to the same kind of mechanical considerations regarding mode of life and depth.

The second of the two discoveries identified above was made by Westermann (1973) amid the burgeoning interest generated by the shell implosion work. Westermann recognized that simple, concave septa found in many orthoconic cephalopods bear striking geometric resemblance to spherically curved, rigid membranes used in such engineering applications as dome, rotunda, and storage tank design. Westermann argued that this similarity should extend to mechanical properties and that, like these structures, the strength of concave septa should be a function of two parameters — radius of curvature and thickness. He measured these parameters in a variety of fossil cephalopods, in Nautilus, and in other modern forms, e.g. Spirula (Westermann, 1973, 1977), and from these data established a method for estimating the living depth of fossil cephalopods. One result of these efforts was to deduce a depth hierarchy for fossil cephalopods in which the depth limits of ancient taxa were set up on the basis of septal geometry. In a series of derivative papers (Westermann, 1975a, 1975b, 1977; Westermann & Ward, 1980), Westermann explored the ramifications of these ideas with respect to the strength of complex, fluted septa, and to the adaptive interplay of shell geometry, septal geometry, and buoyancy. Westermann's work proved to be a provocative and exciting avenue of research because it combined palaeobiologically meaningful results with the attraction of a technique grounded in the apparent quantitativeness of engineering mechanics.

The strength index model has received widespread acclaim as a palaeobathymetric tool. But it is a methodology whose acceptance has outpaced its verification. No sustained programme for testing its tenets or results has been undertaken. Yet the last decade has witnessed collection of a broad spectrum of information which can be brought to bear on the strength index question but whose value in this regard has not been exploited. The bulk of these data involves the natural history, ontogeny, and morphology of Nautilus. This body of data is useful in the present context in two ways: firstly it forms a basis for assessing the status of Nautilus as a reasonable standard of comparison against which to judge fossil forms, and secondly it permits evaluation of the fundamental premises of the model itself.

Our aim in this paper is to discuss these new data as they apply to the strength index concept and cephalopod palaeobathymetry. We will focus on four specific areas of investigation involving Nautilus: ontogeny, septum formation, septal geometry, and shell microstructure. In seeking to determine the extent to which these data support or refute the strength index approach, we hope to place the scientific merits of this concept in the proper perspective.

**Strength index model**

The strength of a three-dimensional object, i.e. the stress under which it fractures or fails, depends on its shape, and on the mechanical properties of the material out of which it is made. The geometrical aspect of strength is of particular interest to structural engineers and architects. The curvilinear shells often involved in their creations are especially noteworthy here because of their resemblance to cephalopod septa.

Engineering shells are curved sheets in which thickness (δ) is small relative to radius of curvature (R). Generally δ/R is less than 0.05. Shells are extremely effective in withstanding stresses produced by loads distributed uniformly across their surface, e.g. hydrostatic pressure, because such loads are transformed into forces acting within the plane of the shell (Fig. 1). Disruptive radial stresses are minimized. Under the action of uniformly distributed normal forces like hydrostatic pressure, spherical shells achieve uniform
strength when their thickness is constant. This would appear to be the underlying design feature of simple, concave cephalopod septa according to Westermann (1973).

The in-plane stress elicited in spherically curved shells subjected to a radial pressure gradient can be expressed as:

\[ \sigma = \frac{PR}{2\delta} \quad \text{Eq.1} \]

where \( \sigma \) is the in-plane stress in the shell, \( P \) is the pressure head across the shell, and \( R \) and \( \delta \) are defined as above. This expression holds for all types of spherical shells including complete spheres, hemispheres, and smaller spherical sections. However, it does not describe stress in regions where curvature changes, holes or gaps occur, or where supporting elements are attached, because these conditions induce significant radial bending stresses which add to in-plane stresses acting at these sites. These regions of stress concentration, or boundary zones, may require such design modifications as thickening of the shell or attachment of buttresses, or tension rings, to ensure the shell's integrity with respect to these added loads. More complete discussion of shell design features can be found in texts on solid mechanics (e.g. Freudenthal, 1966), and on structural design (e.g. Den Hartog, 1952; Schodek, 1980).

Equation 1 can be written in the form

\[ P_{\text{max}} = 2 \sigma_{\text{max}} (\delta/R) \]

where \( \sigma_{\text{max}} \) is the maximum stress a shell can withstand without failure, and \( P_{\text{max}} \) is the pressure acting to produce this stress. For spherically curved shells \( \sigma_{\text{max}} \) is a function of the mechanical properties of the material components of the shell. Westermann (1973) noted that since spherically curved cephalopod septa are composed of the same material, \( \sigma_{\text{max}} \) should not vary widely among cephalopods, and therefore should not be critical in determining relative failure pressures in any suite of specimens. Hence, in such a comparison, \( P_{\text{max}} \) would depend only on \( (\delta/R) \). Westermann (1973) argued that one can use the value of \( P_{\text{max}} \) for Nautilus (about 80 bars) to 'calibrate' this relation between septal geometry and strength. Westermann (1973) then defined a septal strength index, \( SI = (\delta/R) \times 1000 \), as a useful tool for estimating cephalopod depth limits. Since other factors (e.g. material properties) are assumed to be invariant, or inconsequential, in Westermann's model, figures for living depth can be obtained directly from a shell's strength index relative to that of Nautilus. Thus, an animal with a shell having SI = 12, which is about half that of Nautilus (Westermann, 1973), will have a maximum living depth of about 375-400m instead of the 750-800m limit that characterizes Nautilus (Ward & Martin, 1980; Kanie et al., 1980; Ward et al., 1980). This procedure finds maximum limits only; the modal depth range of Nautilus is much less than its depth limit (Saunders & Spinosa, 1979); Ward et al., 1977; Ward et al., 1984; Saunders, 1984a).

As conceived by Westermann, the strength index model is straightforward, based on good engineering practice and productive palaeobiologically useful results. But, at the same time, it is predicated upon several assumptions, which as working hypotheses are not unreasonable, but which must be fully evaluated in order to establish confidence in the results of the technique. The most far-reaching of these assumptions are: 1. septa are truly spherical in the engineering sense, 2. septal boundary zones (suture, septal neck) are mechanically inconsequential, and 3. shell composition and, ultrastructure, and hence material properties are uniform among cephalopods. Much of what follows springs from uncertainties connected with these assumptions.
Ontogeny, strength index, and living depth

To be useful in interpreting cephalopod palaeobathymetry, strength index must be correlated to living depth. Thus, the strength index of a septum should, if the model is reliable, give a reasonable representation of the animal’s living depth at the time the septum becomes functional in withstanding stress. This occurs during chamber formation. As fluid is pumped out of a newly formed chamber, gas diffuses into the void created by fluid removal. Since the pressure of this gas is low compared to ambient hydrostatic pressure (Denton & Gilpin-Brown, 1966), a strong pressure gradient must be set up at the moment gas first appears in a chamber. Knowledge of the chamber formation process gained through X-radiography of growing animals (Ward et al., 1981; Ward & Chamberlain, 1983; Ward, 1985), shows that gas appears in a new chamber during secretion of the adjacent septum. For our purposes, therefore, a septum becomes functional contemporaneously with its formation. Adhering to the model, we can consequently view the sequence of septa in a shell as preserving, in the form of septal strength indices, a record of the animal’s living depth throughout its growth history.

This idea serves as a convenient test of the strength index model because depth predictions generated by the model can be compared to the actual living depths of Nautilus at various stages of its ontogeny. In this regard, Westermann’s data on Nautilus septal geometry (Westermann, 1971, fig. 9; Westermann, 1973, fig. 7) indicate by sharp changes in slope of the plotted trend lines that living depth changes during ontogeny.

To examine this point more fully we measured strength index in the shells of 9 submature to mature, freshly killed specimens drawn from our stock of live animals maintained at the New York Aquarium. All of these shells had at least 30 septa, except one specimen with only 29 (see Chamberlain & Chamberlain, 1985, table 1 for a fuller description of these specimens). Strength index was measured following the procedure of Westermann (1973). We measured septal thickness at a point two-thirds of the distance between septal neck and venter, and we determined curvature radius over the central, spherically curved portion of the septum as in Westermann (1973, fig. 6).

Fig. 2 shows some results of these measurements. Strength index can be seen to vary widely, but systematically, during the course of ontogeny. The pattern of strength index variation found in this shell — increase in the earliest formed septa, declining index in subsequent septa, followed by an increase as maturity is approached — occurs in all the specimens examined, although it is not always as pronounced as in Fig. 2. The final septum in the sequence may give a low strength index value. In submature specimens, such as the one on which Fig. 2 is based, this undoubtedly derives from the slow rate at which newly formed septa achieve their final thickness (see Ward et al., 1981; Ward & Chamberlain, 1983). Such low values can thus be excluded from the general trend. In mature animals (i.e., those with approximated final septa), the decline reflects a real departure from the general pattern of strength index increase in this latter part of the septal sequence.

In analyzing these patterns, we find it convenient to segregate the phragmocone into two distinct regions: 1) embryonic (septa 1-7), and 2) juvenile (septum 8 — last, approximated septum). In submature animals like that in Fig. 2, the adult stage as defined by an approximated, ultimate septum, is lacking.

Embryogenesis

Morphological data on egg size in Nautilus, on shell geometry and ornamentation, and septal placement (Willey, 1897a, 1897b; Stenzel, 1964; Eichler & Ristedt, 1966; Davis & Mohorster, 1973; Haven, 1977; Cochran et al., 1981; Oba & Tanabe, 1983) and oxygen isotope data (Cochran et al., 1981; Landman et al., 1983; Taylor & Ward, 1983) give strong support to the idea that the first seven septa are deposited while the embryo develops within the egg.

The increase in the strength index seen in these embryonic septa (see Fig. 2) implies that living depth increases during embryogenesis.
This, however, is not possible. Bathymetric change cannot occur because the egg develops within a double-walled, horny egg-case which the female firmly attaches to the substrate (Fig. 3). Embryonic septal geometry would therefore not seem to substantiate the strength index model.

This difficulty has not gone unnoticed. Westermann (quoted in Landman et al., 1983), for example, argues that embryonic strength index is an invalid test of the model because the chambers of the embryonic shell are supposedly filled with water, thus precluding a pressure gradient across the septa. The rationale offered for this view is that if the camera contained gas (and hence a pressure head), the buoyancy thus generated would detach the egg from the substrate. This is unlikely. Egg-cases produced by the specimens we maintain, are so firmly anchored that they can be freed only by forceful prying with a knife blade. Moreover, if the animal were to hatch with chambers filled, its overwhelmingly negative buoyancy would preclude normal locomotion, and perhaps compromise food acquisition for the time needed to remove this fluid (several weeks to a month or more judging from the ontogenetic effects of siphuncle geometry and pumping rate described by Chamberlain, 1978a, Ward, 1982, and Chamberlain & Moore, 1982).

There is another argument against Westermann’s claim. Siphuncular microstructure in the embryonic part of the shell does not seem greatly different from that observed in the post embryonic siphuncle (see Mutvei, 1964; Erben et al., 1968, 1969; Blind, 1976; Bandel & Boletzky, 1979). This would suggest that the siphuncular tube in the first seven chambers is functional during embryologic development and that the first several chambers may well contain gas during the earliest phases of ontogeny.

Fig. 2. Ontogenetic variation of Nautilus septal strength index plotted as a function of septum number as counted from shell apex. Each symbol represents one septum. Open symbol represents data from septum that probably had not yet reached its final thickness. Line fitted by eye.
Observations relevant to the existence of embryonic cameral gas are not available. We simply do not yet know whether gas is present during construction of the embryonic shell. The main point we wish to raise is not, therefore, to repudiate Westermann's claim, but to emphasize that present knowledge of Nautilus embryogenesis is not sufficiently advanced to discriminate decisively between contrasting viewpoints. Until the situation improves, Nautilus embryogenesis will provide little tangible assistance in validating the strength index model. Reference to this sphere should therefore be avoided, or disregarded when made.

It is, however, worth noting that if the embryonic shell does not contain gas as Westermann postulates, a new difficulty arises for the strength index model — that of satisfactorily explaining curvilinear septal geometry in septa that are not load-bearing. The problem is this: if the embryonic chambers are emptied of liquid after or just prior to hatching, then only the last-formed (i.e. 7th) embryonic septum will actually receive a hydrostatic load through the back of the body. This being so, it becomes necessary to explain the fact that non-loadbearing septa (septa 1-6) physically mirror hydrostatically stressed septa (septa 7 — last formed). An obvious response, deriving from Seilacher's (1975) and Westermann's (1977) notion that posterior body shape and septal curvature are correlated, is that the embryonic septa simply take on the shape of the rear of the body mass. This is clearly not helpful in the present context because in accepting this idea, one must then also accept the possibility that septal geometry primarily reflects body shape throughout the animal's entire growth history, or, in short, that septal geometry in the whole phragmocone reflects exigencies of body shape rather than representing a solution for withstanding hydrostatic stress. The underlying difficulty is the need to force different functional explanations on portions of a developmental continuum. In accepting the strength index model under the restriction of a fluid filled embryonic shell, one must be willing to say that the embryonic septa are either not functional, or function differently from post-embryonic septa, while at the same time recognizing that these septa belong to the same constructional programme producing the curvilinear stress-resisting septa in the post-embryonic shell. While one can not dismiss the possibility that this actually occurs, its documentation does present an additional, formidable impediment to the strength index model.
Juvenile stages

The decrease in strength index of the early juvenile septa (septum 8 to about 18) plotted in Fig. 2, followed by an increase in later septa, implies that living depth decreases after hatching and the increases again as animals progress toward maturity. Although living depths of juveniles are poorly known, trapping records (Ward et al., 1977; Ward & Martin, 1980; Saunders & Spinosa, 1978; Saunders, 1983, 1984a, 1984b) suggest that juveniles, at least from about the 20th septum onward, occupy the same habitat as the adults, since they are captured with adults in the same traps. In fact, Ward & Martin (1980) found that in the natural populations they studied, juveniles appeared to be more common in the deeper traps.

The observed depth distribution is not what one would predict from septal geometry. Juveniles with about 20-28 septa, have strength indices considerably lower than those of adults and late stage pre-adults (see Table 1), and thus on this criterion should inhabit shallower water than their older conspecifics. This apparent discrepancy between predicted and actual living depth does not instill confidence in the strength index model.

Septum formation

Events in the chamber formation cycle are of interest with regard to septal strength index. Radiography of growing juveniles (Ward et al., 1981; Ward & Chamberlain, 1983) shows that during chamber formation, removal of cameral water, and appearance of cameral gas, begins before the new septum reaches its final thickness. For N. pomptilius cameral emptying commences when septa are only about 50% of their ultimate thickness (Ward & Chamberlain 1983, fig. 3). For N. macromphalus this figure ranges from 25% to 60% (Ward et al., 1981, fig. 5). Table 2 summarizes these data on septal thickness and gas appearance.

In as much as a fully developed hydrostatic pressure gradient is created at the instant that gas first diffuses into a chamber, it is quite apparent that septa become fully functional in resisting hydrostatic pressure at thicknesses much less than that which they ultimately attain. From this we infer that septa can withstand ambient pressure at thicknesses much less than their final value. It would appear that septal thickness at the moment of initial gas influx (i.e. initiation thickness) is more likely to be a crucial parameter in determining septal failing strength than final thickness. The procedure of calculating strength index and inferring living depth from final septal thickness — the procedure which has been the accepted practice in these matters — thus grossly distorts any potential relation between strength and thickness. This result is, in our view, devastating to the strength index model. Numerical values for living depth calculated in the usual way are undoubtedly greatly misleading.

Before proceeding, we wish to discuss two counter-arguments which may be interpreted as lessening the force of this conclusion. First, one may point out that the radiographic work cited above was conducted on captive animals held in surface aquaria. Differences between the experimental and natural environment, notably pressure, or the X-radiation itself, might have induced the radiograph specimens to deposit septa in an unrepresentative fashion. We find this view unconvincing for two reasons: 1) it denies the validity of a large body of aquarium based data (Ward et al., 1981; Chamberlain & Moore, 1982; Ward & Chamberlain, 1983; Zann, 1984; Chamberlain & Pillsbury, 1985; Chamberlain & Chamberlain, 1985; Ward, 1985) on diverse aspects of Nautilus buoyancy control and life habits, which are internally consistent and reproducible, and which give little sign of

<table>
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<th>Ontogenetic Stage</th>
<th>Septa #'s</th>
<th>N</th>
<th>Mean SI</th>
<th>Std Dev</th>
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<td>juvenile</td>
<td>20-28</td>
<td>75</td>
<td>30.3</td>
<td>8.4</td>
</tr>
<tr>
<td>sub-adult</td>
<td>29-32</td>
<td>19</td>
<td>42.0</td>
<td>8.9</td>
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Table 1. Strength index values for juvenile and sub-adult septa in Nautilus. Septum #'s — sequence number of septum as counted from shell apex. N-total number of sampled septa. Mean SI — mean strength index, St Dev — standard deviation. Use of student's t-test shows that the means of the two populations are significantly different ($p<0.02$).
seriously disturbing the chamber formation mechanism, and 2) tests done specifically to evaluate the effects of radiography on growing juveniles (Ward et al., 1981) could discern no significant deleterious effects on chamber formation or growth rate.

The second counter-argument involves the notion of a safety margin. The design of load-bearing structures usually incorporates a failure stress exceeding expected operating loads by several times. In thus 'over-designing' a structure, engineers can obviate much of the danger of the structure failing under normal loading conditions. Organic design emphasizes the same principle. For example, Elliott (1965) found that rabbit tendon has a tensile strength about 5 times that of the tensile forces that act on it. In the same vein, Wainwright et al. (1976) point out that the strength of the limb bones in vertebrates exceeds normal antagonistic forces by a factor of 5. *Nautilus* frequents depths up to about 400m (Saunders & Spinosa, 1979; Ward et al., 1977; Saunders, 1984a; Ward et al., 1984). Since shell failure occurs at a maximum pressures of about 80 bars (about 800m depth), *Nautilus* could be said to have a safety factor of about 2.

One could point to the thickening of septa occurring after cameral gas first appears, as comprising a part of this safety margin strategy. This idea, is, however, almost certainly wrong because it overlooks the facts of the chamber formation cycle. A specific septum will function in resisting hydrostatic pressure conveyed through the body tissues only as long as it is the ultimate septum. Secretion of a new septum and emptying the new chamber of liquid will transfer hydrostatic functioning to this new septum. Thus, a septum functions in resisting body-conveyed pressure between the initiation of emptying of its own chamber, and initiation of emptying in the next-formed chamber. During virtually all of this time, actual septal thickness lies well below ultimate thickness, which is achieved only in the final phase of the chamber formation cycle (Ward et al., 1981; Ward & Chamberlain, 1983). Applying these observations to each septum in turn discloses that during virtually the entire growth history of an animal, hydrostatic stress is resisted by septa with actual thicknesses well below their ultimate thickness. The implication of this is clear. The two-fold safety margin enjoyed by *Nautilus* is built into the septum before emptying begins. Initiation thickness of a septum determines safety margin. Ultimate thickness is not mechanically significant in terms of hydrostatic stress.

Seen in this light, septal thickening occurring after the start of cameral emptying would appear to be produced by some other facet of ontogeny. Our view is that such thickening may be related to instantaneous growth rate or changing buoyancy requirements, or perhaps to both acting in concert. Thus the adaperturally directed pattern of increasing final septal thickness seen in the phragmocone of *Nautilus* may reflect the age-related decline in growth rate documented by Ward & Chamberlain (1983), Saunders (1983; 1984b), Cochran & Landman (1984), and Ward (1985). Our thought is that as growth rate declines and chamber formation period lengthens, final septal thickness may increase as an inevitable consequence of a relatively constant biomineralization rate coupled with the successively longer time the posterior mantle remains in contact with each new septum. Alternatively, septal thickening may relate to buoyancy control, in particular, to the need to offset the greater buoyancy of volumetrically larger chambers formed as growth proceeds, by increasing the deadweight mass through correspondingly thicker septa. The problem may, in short, be a matter of scale. Septal thickness must scale in proportion to cameral length in order to keep the ratio of septum weight to camera buoyancy constant. Although septa probably comprise only about 4-5% of the total weight of the shell (Trueman, 1941; Raup & Chamberlain, 1967) the animal is normally negatively buoyant by less than 1% of its total weight (Ward et al., 1977). Shifts in septal thickness of the magnitude discussed here (about 50%) may thus be crucial in overall buoyancy maintenance.

A final aspect of septal thickening needs elucidation. If a specific thickness of additional septal material were deposited subsequent to the first appearance of cameral
gas, it might still be possible to use the strength index model because we would then have a means of relating the readily measured parameter of final septal thickness (but one having little significance in terms of hydrostatic stress) to the actual critical stress parameter (initiation thickness). To do this would require the following: 1. knowledge of the ratio between initiation thickness and final thickness, and 2. assurance that this ratio is constant not only for Nautilus, but for cephalopods generally, or that it may be independently determined in fossil forms. Two points weigh against this position. Firstly, the data for N. macromphalus (Table 2) do not support it. The wide range in initial septal thickness, in specimens with approximately equal numbers of chambers and caught at the same depths, means that at least for this species of Nautilus, no species-wide thickness coefficient relating these two thickness parameters is likely to exist. Secondly, claims about safety margins and thickness coefficients in fossil forms are unfounded, and at best, premature. There is a complete absence of fossil data bearing on these questions. With regard to safety margins, in particular, it seems likely that cephalopod shell design made provision in fossils for such a feature but how to determine it is unknown. There is at present no acceptable means of applying the safety margin concept to fossil cephalopods while preserving any hope of the quantitiveness prudence requires.

Septal geometry and strength

Two important corollaries can be deduced from the central theme of the strength index concept: 1. in a suite of septa simultaneously subject to high hydrostatic pressure, the one having the lowest strength index should fail first, and 2. the failure pressure of a suite of fractured septa should vary directly with strength index. Data reported by Chamberlain & Chamberlain (1985) who examined septal fracture in Nautilus are useful in analyzing these two ideas.

With regard to the former point, these authors tested septa in fresh N. pompilius shells by filling chambers with water under high hydrostatic pressure (see Chamberlain & Chamberlain, 1985 for a fuller description of this experiment). Pressure was elevated until a septum ruptured. Although this technique does not strictly simulate the loading regime acting on a shell in life, it did produce, in a majority of cases, the characteristic tensile failure occurring under normal loading conditions. The strength index of the ruptured septum was then compared to those of septa left intact at the conclusion of the test. Their results, as they apply here, are summarized in Table 3. It is apparent from these data that in none of the specimens tested did the septum with the lowest strength index actually fail. In fact, in two specimens (A1 and F2) the septum having the highest strength index ruptured. In no case was the weakest septum as defined by its strength index actually the weakest septum.

Fig. 4 plots data on rupture pressure and strength index that bears on the second point.

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**Table 2. Thickness of septa when gas first appears in adjacent chamber.** Species: P — N. pompilius; M — N. macromphalus. Each entry reports data from one shell. Initial thickness — thickness of septum at first appearance of cameral gas expressed as a percentage of thickness of previous specimen. References: 1- Ward & Chamberlain, 1983; 2- Ward et al., 1981.

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<th>Species</th>
<th>Initial Thickness</th>
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<tr>
<td>P</td>
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</tr>
<tr>
<td>P</td>
<td>49</td>
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<td>P</td>
<td>50</td>
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<td>8</td>
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<tr>
<td>M</td>
<td>59</td>
<td>9</td>
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**Table 3. Strength indices of ruptured and intact septa in N. pompilius shells studied by Chamberlain & Chamberlain (1985).** N total number of septa in samples — SI Range — limits for range of strength index values in septal suite studied. SI Frac. Septum — strength index of septum that fractured.

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<th>Shell</th>
<th>N</th>
<th>SI Range</th>
<th>SI Frac. Septum</th>
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<td>A4</td>
<td>8</td>
<td>57-32</td>
<td>33</td>
</tr>
<tr>
<td>F2</td>
<td>7</td>
<td>38-23</td>
<td>38</td>
</tr>
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<td>F4</td>
<td>13</td>
<td>47-28</td>
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noted above. The data are widely dispersed, so much so that the linear regression fitted to this scatter \( y = -0.99X + 81.4 \) gives a correlation coefficient of only \( r = 0.234 \). The two parameters do not appear on this ground to be strongly correlated. In particular, no firm basis can be seen for claiming that strength index is a reliable indicator of rupture pressure. Estimates of cephalopod palaeobathymetry based on septal strength index do not therefore appear well founded.

Shell microstructure and strength

Shell microarchitecture among molluscs varies widely (e.g. Kennedy et al., 1969; Taylor et al., 1969), and plays a significant role in determining the mechanical properties of the molluscan skeleton (Taylor & Layman, 1972; Currey & Taylor, 1974; Currey, 1976). It is, however, a fundamental assumption of the strength index model that the microstructure of the hard tissues in cephalopods is taxonomically and phyletically uniform. Microstructural uniformity is necessary for two reasons: 1. little is known about the effects of microstructure on cephalopod shell mechanics, and 2. without such knowledge, determining living depth solely on the basis of septal geometry makes poor sense unless one negates the potentially obscurant effects of the structural component by asserting that they are unimportant.

Recently, Mutvei (1983) has revealed some startling disparities in shell microstructure between Nautilus and the Ordovician nautiloid Isorthoceras suggesting that cephalopods, like other molluscs, are not homogeneous in this characteristic as had been thought. Mutvei observes that the spacing of stacks of carbonate tablets comprising the shell nacre in the two species differs markedly. Differences in spacing of the skeleton's framework elements, of the magnitude observed by Mutvei (1983, fig. 4), and concomitant differences in the distribution and relative
abundance of organic matrix, suggest that material strength in these two species must differ, as Mutvei notes. Following Mutvei, Isorthisceras may be weaker due to its more widely spaced framework, or it may be quite strong since skeletal strength increases with organic content in many groups with composite skeletons (Chamberlain, 1978b, table 2). In any event, Mutvei’s observations demonstrate the inaptness of this fundamental assumption upon which the strength index model rests.

Status of the septal strength index

In the previous pages, we have identified facets of the life history and morphology of Nautilus which can act as tests of the septal strength method of estimating cephalopod living depth. Our analysis of these tests is as follows:

Embryogenesis. Septal strength index increases adaptically in the embryonic septa (septa 1-7). According to the strength index model, this means that the developing embryo moves into deeper water as embryogenesis proceeds. This is not possible because the embryo develops within an egg case which is firmly attached to the substrate and consequently immobile. Depth changes of the kind required by the model are not possible. However, further information on embryogenesis is needed before this can be regarded as convincing.

Juvenile stages. Juvenile development in Nautilus is characterized by shifting patterns of change in septal strength index. From the early neo-natal septa (septa 8-10) to about the 20th septum, the pattern is one of decreasing strength index. From this point to the last-formed septum, septal strength increases. The strength index model would predict from these trends an initial decrease in living depth during the early phases of ontogeny, followed by increasing living depth in later stages. Although depth preferences of living Nautilus populations are not fully known, capture records presently available indicate that at least from the 20-25th septum onward, juveniles and adults share the same habitat. The reality of juvenile living depth thus contradicts the predictions of the model.

Septum formation. Depth estimates calculated from strength indices are based on values for the thickness of fully formed, complete septa. Yet, in Nautilus gas appears in newly formed chambers long before septa reach their final thickness. Hence, in Nautilus septa are exposed to ambient pressure when only partially complete, and therefore must be strong enough to withstand this pressure when septal thickness is a small fraction of its final value. In relying on final thickness, the septal strength index is clearly misapplied and, at best, grossly distorts living depths computed for fossil forms. Since septal thickness at initial application of pressure appears to vary across suites of septa and specimens, no utilitarian means seems to exist for developing a quantitative ‘safety margin’ based on excess septal thickness which can be applied to fossil septa.

Septal geometry. Experiments with fresh Nautilus shells indicate that in a series of septa exposed to elevated hydrostatic pressure, the weakest septum as defined by actual failure is not the weakest septum as defined in terms of strength index. Failed septa in such sequences have higher strength indices than many septa that do not fail. In addition, among failed septa, there is no correlation between failure pressure and strength index.

Shell microstructure. In determining septal strength solely on the basis of septal geometry, the strength index tacitly assumes uniformity among cephalopods in mechanical properties of the septal material. However, analysis of shell microstructure reveals that mechanical uniformity is not likely to be widespread among cephalopods with simple septa. At least one Ordovician nautiloid, Isorthoceras, has a microstructure so unlike Nautilus, that assumption of uniformity seems patent unwarranted.

Taken together, these considerations form a convincing body of evidence challenging the veracity of the septal strength index model. Our arguments attack the strength index model in two major ways: 1. they repudiate Nautilus as a reasonable paradigm upon which to base depth calculations for fossil cephalopods, and 2. they question the logical foundations upon which the model is formulated. In the first case, Nautilus septal strength consistently fails to conform to the precepts of the strength index concept. This
indicates quite clearly that the 800m depth limit of Nautilus should not serve as a standard for computing depth for fossil cephalopods. But our analysis goes further. It gives support to the even stronger conclusion that the model itself is seriously flawed. In this regard, the model’s shortcomings are evident with respect to: 1) adopting a functionally irrelevant septal thickness parameter, and 2) relying on the false assumption of constancy in material properties of shell and septa across a wide array of taxa. There is yet a third point. When the shell of Nautilus ruptures under pressure, the site of initial failure is usually the septal suture (Chamberlain & Chamberlain, 1985). Consequently, the septum does not appear to be the weak point of Nautilus shell design. Since fossil cephalopods with simple septa have sutural configurations not unlike that of Nautilus, we believe that this caveat applies to cephalopods generally. In basing strength index on septal geometry rather than sutural characteristics, the strength index model misidentifies the real source of failure.

Is cephalopod septal strength index an index of cephalopod septal strength? Apparently not.

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