FLUID TRANSPORT PROPERTIES OF *NAUTILUS* SIPHUNCULAR TUBE: WITHIN-CAMERA DISTRIBUTION OF FLOW RATE

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ABSTRACT. There are two viewpoints concerning the nature of flow across the siphuncular tube of *Nautilus* and other ectocochliates: (1) flow is uniform along the length of the tube; (2) flow is mainly localized in the septal necks. We tested these alternatives in specimens of *N. pompilius* by measuring flow rates through septal necks sealed with epoxy. We found that the septal neck, and specifically the so-called pillar zone, is not a conduit for fluid transport. Fluid entering or exiting the camerae flows uniformly through the permeable conchiolinous membranes of the connecting ring. This situation is the result of two factors: (1) the connecting ring is provided with osmotically active epithelial cells whereas the septal necks are not; and (2) the pillar zone is not porous, but consists of a solid array of crystal matrix intergrowths. The actual function of the pillar zone appears to lie in the direction of optimizing the mechanical strength of the septum-connecting ring junction and of minimizing the metabolic cost of constructing the connecting ring. The microstructure of the septal neck in many fossil cephalopods is consistent with this interpretation. Evaluation of siphuncle function and adaptation in fossil forms, and of evolution in siphuncular structure, must take account of the fluid transport properties of the connecting ring.

BUOYANCY control in *Nautilus* occurs by a process of local osmosis initiated by the epithelial cells lining the inner side of the siphuncular tube (Denton and Gilpin-Brown 1966, 1973; Denton 1971, 1974; Greenwald *et al.* 1980; Ward 1980; Greenwald *et al.* 1982). Fluid flows into or out of the camerae in response to the relative osmolarity of the water reservoirs on opposite sides of the siphuncular tube (cameral water and intracellular fluid respectively). Since fluid must pass through the wall of the siphuncular tube, fluid transport properties of the tube are of paramount importance in buoyancy regulation. Collins and Minton (1967) Chamberlain (1978), and Chamberlain and Moore (1982) have examined tube transport by introducing water under high hydrostatic pressure into the siphuncular tubes of freshly killed animals. Measurement of the passive flow thus induced suggests that the permeability coefficient of the tube is very low ($\sim 2{\cdot}4 \times 10^1$ μd; Chamberlain 1978), but that this is sufficient to provide flow rates up to about three orders of magnitude greater than the rates of osmotic flow actually observed in live animals (Chamberlain and Moore 1982). The transport capacity of the tube apparently provides no significant impediment to fluid movements necessary for buoyancy control.

Implicit in this experimental work on osmotic flow and tube transport has been the view that within a chamber, fluid movement is roughly uniform along the length of the tube. No specific portion of the siphuncular tube has been recognized in these efforts as accounting for the bulk of fluid transport (text-fig. 1A). This notion has recently been challenged by Bandel and Boletzky (1979), who assert that fluid transport is centred primarily near the contact between the septal neck and siphuncular tube (text-fig. 1B). According to these authors, pillar-like structures lining the adapertural surface of the nacreous layer in the septum continue into the septal neck (text-fig. 2). On the basis of its apparently open, portico-like structure, Bandel and Boletzky identify this pillar zone of the septal neck as being highly porous, much more so than the conchiolinous horny tube, and suggest therefore that the pillar zone must be the primary conduit for fluid transport across the siphuncle.

The pillar zone theory has been amplified by the discovery (Obata *et al.* 1980; Bandel 1981; Tanabe *et al.* 1982) that pillar zones seem to occur in a variety of fossil ectocochliates as well as in *Nautilus*.

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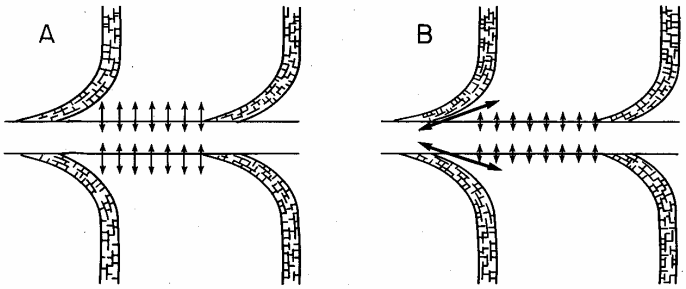
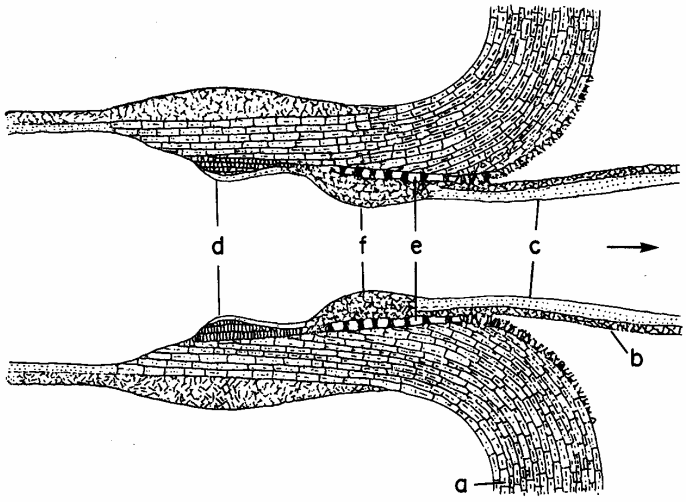


TEXT-FIG. 1. Contrasting models of relative flow rates across siphuncular tube. Arrow lengths indicate approximate magnitude of flow at specific sites along tube. A, uniform flow theory. B, localized pillar zone flow theory of Bandel and Boletzky (1979).

Further support is given to Bandel and Boletzky's claim by the presence of pillar zones through which fluid undoubtedly flows in sepiid cuttlebone and in the siphuncle of *Spirula* (see Bandel and Boletzky 1979).

PALAEOBIOLOGICAL IMPLICATIONS OF PILLAR ZONE FLOW

The question of whether fluid transport occurs uniformly along the siphuncular tube or preferentially through the pillar zones is one of considerable importance in interpreting the functioning of the ectocochliate buoyancy mechanism. In particular, comparisons of siphuncular microstructure, as represented in Palaeozoic nautiloids and *Nautilus* (Mutvei 1972*a*, *b*) or among nautiloids and ammonoids (Birkelund and Hansen 1968, 1974; Mutvei 1972*a*, *b*; Kulicki 1979; Obata *et al.* 1980; Bandel 1981; Tanabe *et al.* 1982), will of necessity take on different meanings according to the weight assigned to the two opposing views of fluid transport. Most importantly, analysis of the adaptive significance of the varied septal neck geometries seen in fossil cephalopods, or of connecting ring structures, as observed for instance in the Devonian nautiloid *Archicoceras* (Crick and Teichert 1979), would lead to radically different viewpoints depending on how one interprets the presence or absence of pillar zones and their role in cephalopod buoyancy. If pillar zone flow of the kind



TEXT-FIG. 2. Longitudinal section through siphuncular tube and septal neck of *Nautilus pompilius* (after Bandel and Boletzky 1979, fig. 21). *a*, septal nacre; *b*, chalky layer; *c*, horny layer; *d*, inner ridge; *e*, pillar zone; *f*, spongy region.

advocated by Bandel and Boletzky actually occurs, then connecting ring permeability and geometry become meaningless flow transport parameters because fluid movement, being centred in the septal necks, would largely bypass the rest of the siphuncular tube. If we accept the pillar zone model, we must reject the analyses of siphuncle functional morphology provided by Denton and Gilpin-Brown (1966), Collins and Minton (1967), Chamberlain (1978), Chamberlain and Moore (1982), and Ward (1982).

AIM OF THIS WORK

The question of siphuncle flow localization raised by Bandel and Boletzky (1979) is clearly a significant one for ectocochliate biology. Yet, in the five years since their paper has appeared no effort has been made to substantiate the position advocated in it through analysis of tube flow properties. The growing acceptance of the localized flow theory among some cephalopod specialists is based only on intuition concerning the apparent porous nature of the pillar zone, and on uncertain analogy with siphuncle function in endocochliates. In this paper we report results of an experiment dealing with hydrostatically induced flow through open and sealed septal necks of *N. pompilius*. It is our purpose to provide data that will help discriminate between these contrasting alternatives.

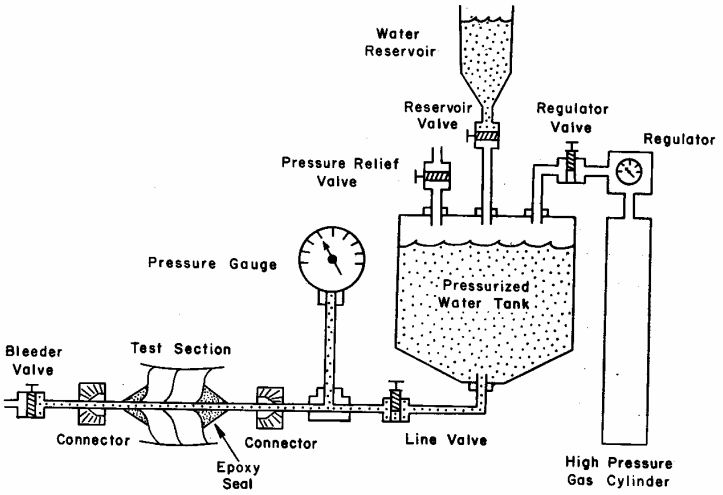
MATERIALS AND METHODS

Our testing procedure is based on that devised by Chamberlain and Moore (1982) for measuring siphuncular flow rate in *Nautilus* shells. Two fresh shells, described in Table 1, were sectioned about 1 cm from the mid-plane to reveal the siphuncle. Using forceps, we extracted the siphuncular tissue from the tube and then attached a ten to fifteen chamber length of tube, still wet, undecayed, and intact in the shell, to our testing apparatus. This consists of three main components (text-fig. 3): (1) a pressurized gas cylinder and regulator for inducing high fluid pressure in the test system; (2) a water reservoir for converting gas pressure to hydrostatic pressure; and (3) instrumentation for reading the pressure of the water in the siphuncular tube. A specimen is connected to the apparatus by inserting a high pressure line from the pressure gauge a short distance into the open septal neck of the outermost septum of the section to be tested, and cementing it in place with epoxy resin. The system is pressurized by releasing gas into the water reservoir. This elevates the hydrostatic pressure in the test section and causes water to flow outward across the permeable wall of the siphuncular tube. Water thus expelled from the siphuncle collects in the camerae from which it is then withdrawn and its volume determined by pipette. Chamberlain and Moore (1982) fully describe the apparatus and basic testing procedure.

TABLE 1. Data for specimens tested in this paper. Test interval = length of time between death of animal and testing.

Specimen	Shell weight (gm)	Shell diameter (cm)	Total number of chambers	Test interval (days)
A	246	11·8	36	2
B	109	8·5	28	0

Our method for identifying the contribution of the pillar zone to overall siphuncular flow consisted of two steps. First, we determined flow rate through fresh tubes prepared only as described above, i.e. with tissue removed. In both specimens listed in Table 1, flow in each chamber of the test section was measured at a variety of pressures from about 10 to 40 bars. Because this testing configuration involves an unaltered tube wall, observed flow rates will reflect the full contribution of pillar zone flow. When unaltered flow rates had been determined in this way, we modified the septal necks in order to interfere with flow through the pillar zone. This was done by mechanically removing the pellicle and chalky layer from the connecting ring and septal neck,

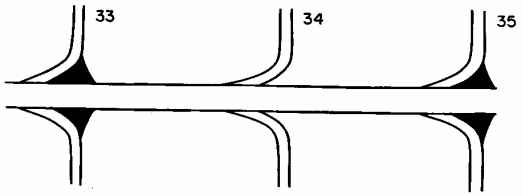


TEXT-FIG. 3. Testing apparatus for measuring flow across wall of the siphuncular tube (after Chamberlain and Moore 1982, fig. 1).

and covering the area thus exposed with epoxy. To ensure a watertight seal over the pillar zone, we used a specialized resin called Aquatapoxy, manufactured by the American Chemical Co., Palo Alto, California, which is formulated to adhere to wet surfaces. As indicated in Table 2, we sealed an alternate series of septal necks in the test sections of our two specimens. Text-fig. 4 shows the appearance of a portion of the test section in specimen A after preparation with epoxy. The unaltered necks in these sequences were used for experimental control. After preparation was complete, the sealed–unsealed sequences were tested as described above. Fluid passing through the siphuncular tube was again collected in the camerae and measured. Since the pillar zones in alternate, sealed necks could not now transport water, comparing the volume of water passing through such test segments to the flow through unaltered necks revealed the relative importance of pillar zone flow to overall flow of fluid across the siphuncular tube.

TABLE 2. Sequences of septal necks examined in the two specimens studied here. S—septal necks sealed with epoxy. O—septal necks open (unsealed). Septa identified by sequence number as counted from apex of shell.

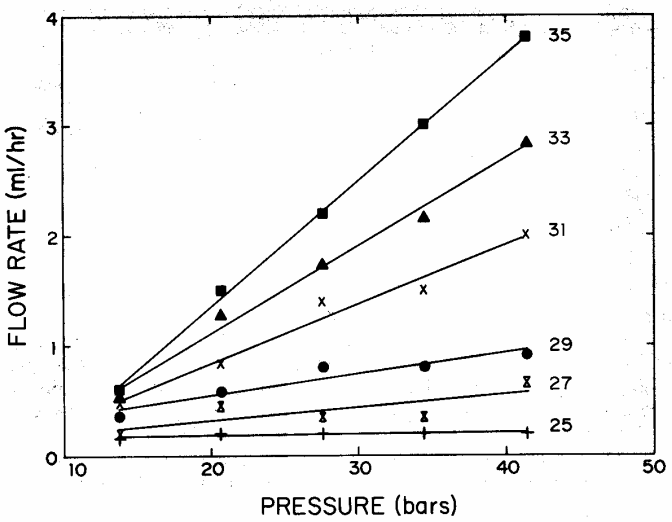
Specimen A	S	35		33		31		29		27		25
	O		34		32		30		28		26	
Specimen B	S	26		24								
	O		25		23							



TEXT-FIG. 4. Test configuration for a portion of specimen A after alternate septal necks (35 and 33) had been sealed with epoxy. Septa numbered in ascending order from shell apex.

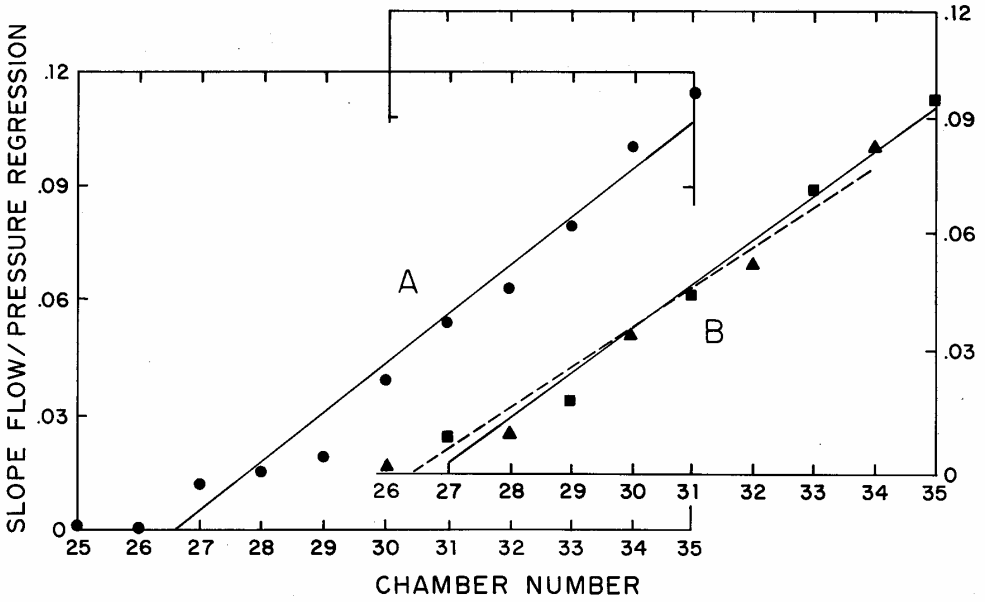
FLOW RATES IN UNALTERED NECKS

Text-fig. 5 shows the relationship between volumetric flow rate and different values of applied pressure for the segment of siphuncular tube in each of six chambers in specimen A. These results apply to the initial series of runs in which none of the septal necks in the test series had been sealed with epoxy. Data for even-numbered chambers in the sequence fall in the appropriate positions between adjacent odd-numbered chambers but have been omitted for clarity. The second specimen yielded similar results.



TEXT-FIG. 5. Siphuncular flow rate plotted as a function of hydrostatic pressure for six chambers in specimen A. Data for unaltered septal necks. Scatter for each chamber fitted with linear regression. Chamber number at right-hand end of each regression line.

Several features of text-fig. 5 are worth noting. First, measured flow rates (~0·5–4·0 ml/hr) are about the same as rates previously obtained for *N. pompilius* (Chamberlain and Moore 1982), and are much higher than osmotic pumping rates in live animals, as these authors point out. Increasing hydrostatic pressure induces higher flow rates in all of the siphuncular segments studied. Flow rate increases linearly with pressure. Note also that tube segments in the volumetrically larger chambers (i.e. those with higher sequence numbers) exhibit higher slopes than earlier formed, smaller chambers. This pattern is seen in the data for all shells so far tested (see Chamberlain and Moore 1982), and would thus appear to respresent the response of normal siphuncular tubes to elevated pressure. The overall behaviour of the test section can be illustrated by plotting the slopes of the curves in text-fig. 5 as a function of the position of each chamber in the sequence of chambers composing the phragmocone. This is done in text-fig. 6A. A simple, linear relation in these parameters is evident over the range of chambers represented in the test section. We would point out that this relation cannot, however, hold over the entire phragmocene because chambers formed early in the sequence cannot vary in slope significantly from chambers 25–26. The relationship for the whole phragmocone is probably some sort of power function similar in form to the relationship between siphuncle surface area and chamber sequence number observed by Chamberlain and Moore (1982) and Ward (1982).

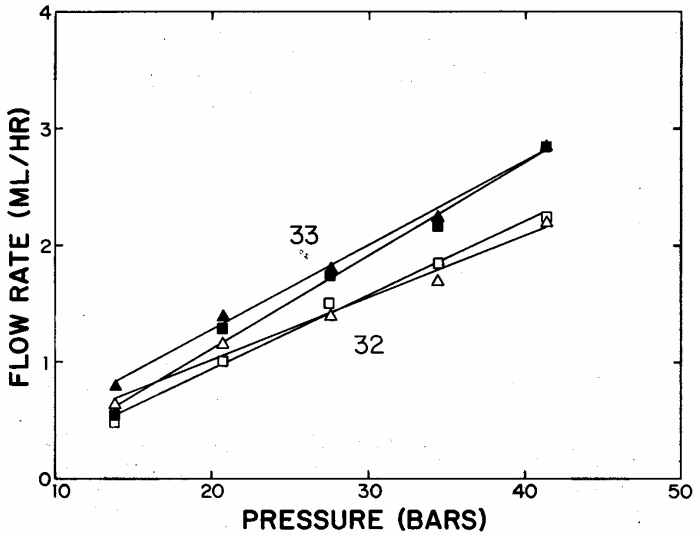


TEXT-FIG. 6. A, slope of flow rate–pressure regressions for tube segment in each chamber of specimen A tested, plotted as a function of chamber sequence number. Chamber number increases toward shell aperture. All septal necks unsealed. B, slope of flow rate–pressure regressions for tube segments in chambers 26–35 of specimen A. Odd numbered septal necks sealed (squares). Even numbered septal necks open (triangles). All data from second test run. Each data set fitted with linear regression as follows: sealed necks (solid line); $y = 0{\cdot}011\ x - 0{\cdot}032$, $r = 0{\cdot}990$; open necks (dashed line); $y = 0{\cdot}010\ x - 0{\cdot}270$, $r = 0{\cdot}985$.

FLOW RATES IN SEALED NECKS

Results obtained for our second series of test runs, in which alternate septal necks (odd numbered ones—see Table 2) were sealed with epoxy, give little evidence of a primary role for the septal necks in cameral fluid transport. Text-fig. 7 shows data for one such sealed neck. Flow rates obtained when septal neck 33 was sealed (solid squares) are little different from flow rates observed when this septal neck was unaltered (solid triangles). Statistical analysis (t-tests) of these two data sets (see Zar 1974, pp. 228–230) are unable to separate either slopes ($p = 0{\cdot}24$) or y-intercepts ($p = 0{\cdot}79$). Within the resolving power of our procedure, the two results are, in effect, identical. Sealing the septal neck with epoxy has no apparent effect on flow. As noted above, if the Bandel and Boletzky flow model were valid, one would expect a significant reduction in flow rate when septal necks are sealed. The absence of such a situation indicates that this model is not correct. Fluid must move across the wall of the siphuncular tube more or less uniformly along its entire length. It is not appreciably localized in the septal necks.

This interpretation is strengthened when we broaden our analysis to include other chambers in the test sequence. Text-fig. 7 also shows data for an adjacent chamber, but one which we left unaltered as a control during both series of tests. Results generated during the first test series (all necks unaltered) are shown as open squares, while data obtained in the second set of runs (odd numbered necks sealed) are indicated by open triangles. In both cases, septal neck 32 remained unsealed, and in both cases the flow data are coincident. Once again, Zar's procedure is unable to discriminate between these data



TEXT-FIG. 7. Flow rate for siphuncular tube segments in chambers 32 and 33 of specimen A. Solid squares—data from initial test series for chamber 33 in which septal neck has not been sealed. Solid triangles-data from second test series for chamber 33 in which septal neck has been sealed with epoxy. Open squares—data from initial test series for chamber 32; septal neck not sealed. Open triangles—data from second test series for chamber 32; septal neck not sealed. Each data set fitted with linear regression as follows: chamber 33 (unsealed neck), $y = 0{\cdot}079\ x - 0{\cdot}480$, $r = 0{\cdot}995$; chamber 33 (sealed neck), $y = 0{\cdot}072\ x - 0{\cdot}164$, $r = 0{\cdot}944$; chamber 32 test series 1: $y = 0{\cdot}063\ x - 0{\cdot}330$, $r = 0{\cdot}996$; chamber 32 test series 2: $y = 0{\cdot}053\ x + 0{\cdot}044$, $r = 0{\cdot}991$.

sets ($p = 0{\cdot}11$ and $p = 0{\cdot}98$ for slopes and y-intercepts respectively). These results show that the overlap seen in the sealed-unsealed data for chamber 33 is not likely to have derived from unrecognized variation in test conditions, i.e. this similitude is not a consequence of a major system-wide fluctuation in some test parameter that fortuitously and precisely offsets a real reduction in flow for the sealed neck. If this were to have occurred, the data for chamber 32 would show it as a separation of the data sets for the two test series. The data for other even-numbered chambers (in which septal necks are left unsealed) give the same results.

Our ideas are also strengthened by pooling our data for all sealed septal necks. Table 3 gives these results as well as the outcome of statistical evaluations of their significance. Again, we rely on regression parameters to express the relation between flow rate and applied pressure. In four of the five cases summarized in Table 3, the slopes of the regressions of the open and sealed test configurations cannot be separated at acceptable levels of significance. In all five chambers, the y-intercepts do not differ. Even in the single instance (chamber 35) where the slopes of the open-neck and sealed-neck regression differ at acceptable levels ($p = 0{\cdot}05$), the magnitude of the difference is small in terms of flow rates. For example, at a pressure of 25 bars, about the median of the range tested and a pressure equivalent to the modal depth range of living *Nautilus* populations (Ward and Martin 1980), flow rates for the two test configurations differ by only 16%. This is not the situation envisaged by Bandel and Boletzky (1979) in elucidating their pillar zone model of siphuncular transport.

Arguments about the character of tube transport that we have advanced so far, involve

TABLE 3. Regression parameters for flow rate–pressure data for odd-numbered chambers in specimen 1. Chamber number = chamber sequence number counted adaperturally from shell apen. Septal neck = condition of septal neck during testing: open—septal neck unsealed, pillar zone flow unimpeded; sealed—septal neck sealed, pillar zone flow shut off. Slope = slope of flow rate–pressure regression for test configuration indicated in column 2. *y*-int. = *y*-intercept of flow rate–pressure regression. Slope Comp. = comparison of slopes for open versus sealed data sets using Zar's (1974) procedure: *t*—*t* statistic calculated for regression comparisons; sig.—significance level of *t*. *y*-int. comp. = comparison of *y*-intercepts for open versus sealed data sets using Zar's (1974) procedure. Degrees of freedom: slopes = 6; *y*-intercepts = 7.

				Slope comp.			y-int.comp.	
Chamber no.	Septal neck	Slope	*y*-int.	*r*	*t*	*sig.*	*t*	*sig.*
35	Open	0·114	−0·940	0·999	2·84	0·05	0·598	0·57
	Sealed	0·095	−0·080	0·993				
33	Open	0·079	−0·480	0·995	1·327	0·24	0·275	0·79
	Sealed	0·072	−0·164	0·994				
31	Open	0·054	−0·236	0·986	1·063	0·33	0·057	0·96
	Sealed	0·045	0·029	0·968				
29	Open	0·019	0·156	0·952	0·357	0·73	0·553	0·60
	Sealed	0·018	0·140	0·984				
27	Open	0·012	0·080	0·768	0·543	0·61	0·686	0·52
	Sealed	0·009	0·120	0·968				

comparisons made between different test runs. We can approach this question also by evaluating data from the same test run. Such data are presented in text-fig. 6B, in which we record the slopes of the flow rate–pressure regressions for all chambers tested in our second test series. Odd-numbered chambers contain sealed septal necks, while even-numbered chambers have open, unsealed necks. Note that data for the two different neck configurations fall in the same general area of the graph. In fact, the slopes and *y*-intercepts of the regressions for the sealed necks (solid line) and open necks (dashed line) cannot be separated at acceptable significance levels ($t_{\text{slopes}} = 0{\cdot}752$, $p = 0{\cdot}48$ at d.f. = 6; $t_{y\text{-int}} = 0{\cdot}62$, $p = 0{\cdot}95$ at d.f. = 7). Sealed necks would thus appear to give the same results as open necks. One would not expect this kind of situation to develop if the pillar zones were the primary conduit for fluid transport. Instead, shutting off pillar zone flow by sealing the septal necks should result in a wide disparity between the sealed and unsealed data. The conformity of the data thus argues convincingly against the pillar zone model.

IS CAMERAL FLOW LOCALIZED IN THE PILLAR ZONE?

The data on flow rates for sealed and unsealed septal necks presented in Table 3 and text-figs. 6 and 7, point quite convincingly to the conclusion that the pillar zone, in spite of its apparent high porosity, is not a major passageway for fluid movement across the siphuncular tube. The tenets of Bandel and Boletzky's pillar zone model of fluid transport are not supported by our data. Instead, fluid would appear to move across the connecting rings uniformly.

This result is a most significant one for interpreting the functions of the siphuncle in *Nautilus*. In this regard, we can now see that the statements made by Denton and Gilpin-Brown (1966), Chamberlain (1978), Ward (1982), and Chamberlain and Moore (1982) involving the role of siphuncle geometry and permeability in controlling fluid transport across the tube wall, cannot be rejected (on these grounds at least) as misapprehended. Fluid moves across the tube wall during episodes of osmotic pumping, not through the pillar zones, so that connecting ring permeability, surface area, and other factors identified by these authors must influence this flow in a substantial way. The results we present here indicate that we should put aside such ideas as pillar zone flow and continue to look

toward the properties of the siphuncular tube wall, and the tissue that underlies it, for a fuller understanding of the *Nautilus* buoyancy mechanism.

These same considerations apply to fossil cephalopods. Analyses of geometry, material properties, composition, and structural features of connecting rings in fossil forms should be sensitive to the effect of such parameters on cameral flow. Evaluation of siphuncle function, siphuncular adaptation, and evolution of siphuncular structure must take account of fluid transport properties. Our own view is that much of the phylogenetic variation observed in these parameters can be explained in terms of fluid transport and in the status of fluid transport as an important determinant of cephalopod mode of life.

WHAT PREVENTS PILLAR ZONE FLOW?

Passage of fluid through the pillar zone in *Nautilus* is precluded for two reasons. First, the histology of the siphuncular epithelium is not compatible with flow of this type. The septal neck is not underlain by tissue capable of solute-coupled transport (Greenwald, pers. comm. 1984), as would be required in order osmotically to pump fluid directly through the pillar zone. Instead, the connecting ring is associated with such tissue, as is indicated in the sample preparation techniques used by Denton and Gilpin-Brown (1966) and Greenwald *et al.* (1982). The intra-cameral portion of the siphuncular tube is furnished with a pumping mechanism, but the septal neck lacks one. This arrangement is antithetical to the requirements for pillar zone flow.

Secondly, the microarchitecture of the septal neck is not compatible with flow through the pillar zone. In this regard the analyses of Mutvei (1972*b*) and Kulicki and Mutvei (1982) indicate that the spherulitic-prismatic layer of the septal neck (roughly equivalent to Bandel and Boletzky's pillar zone) does not lead directly to the siphuncular epithelium but rather is separated from it by the conchiolinous membranes of the connecting ring. Thus, if fluid could be drawn through the pillar zone (or spherulitic-prismatic region) in the absence of active epithelium, its passage would still be constrained by the fluid conductance properties of the horny tube, just as it would be along the entire length of the connecting ring. Kulicki and Mutvei (1982) show that this is also the case in the ammonite *Quenstedtoceras*. Finally, we also point out that recent studies of siphuncle chemistry (Crick, pers. comm. 1984) involving sample preparation techniques specifically geared toward retaining the non-crystalline components of the shell material indicate that the spaces between the crystal stacks in the pillar zone are not fluid filled as Bandel and Boletzky assert, but are filled by organic matrix. The pillar zone is actually solid, and for this reason cannot convey fluid, or at least, conveys it at a rate constrained by the fluid conductance properties of the conchiolinous matrix.

OF WHAT SIGNIFICANCE IS THE PILLAR ZONE?

If the pillar zone in *Nautilus* does not function as Bandel and Boletzky postulate, what purpose, if any, does it serve? Two possibilities present themselves: (1) the pillar zone may optimize the mechanical strength of the septal neck-connecting ring union; and (2) the pillar zone may be a consequence of unusually rapid carbonate secretion linked to the chamber formation cycle. Several observations are compatible with these hypotheses.

The pillar zone lies along the inner surface of the septal neck (text-fig. 2; see also fig. 1 of Mutvei 1972*a*; and fig. 1 of Kulicki and Mutvei 1982). It therefore occupies a medial position between the crystalline nacreous layer of the septal neck and the conchiolinous membranes of the connecting ring, and as such, must serve as a means of attachment for these two siphuncle components. Conchiolin and nacre diverge widely in their mechanical properties—conchiolin is pliant and elastic, while nacre is rigid and brittle (Wainwright *et al.* 1976). Anchoring such disparate materials firmly enough to resist the severe hydrostatic pressure head encountered at the living depth of *Nautilus* may require the kind of intergrowth of crystalline elements and organic matrix observed by Crick (pers. comm. 1984) in the pillar zone. Thus, the pillar zone may be designed to maximize the strength with which the connecting ring and septal neck are joined. Similar crystal-matrix intergrowths are observed in

other examples involving the seating of load-bearing members of different composition, particularly in vertebrate bone and the myostracum of molluscs, in the latter of which carbonate prisms are surrounded by conchiolinous sheaths (Wainwright *et al.* 1976).

Deposition of the pillar zone may also be related to chamber formation. X-ray studies of the chamber formation sequence in live *Nautilus* (Ward *et al.* 1980; Ward and Chamberlain 1983) show that the chamber formation cycle consists of several phases of unequal duration. In this regard, forward movement of the body which occurs in preparation for the secretion of a new septum, requires at the most only about seven days in *N. pompilius* (Ward and Chamberlain 1983). This stage in the chamber formation cycle is a time of rapid secretion of cameral fluid which fills the expanding space between the forward-moving body and the last formed septum. Carbonate and conchiolin, needed to construct the connecting ring and new septum, also are produced rapidly, and there is some evidence (Crick, *et al.* 1984) that the biomineralization system is heavily stressed at this time due to the increased metabolic demands associated with these processes. It is quite plain from the position of the pillar zone in the septal neck, and from its continuity with the prismatic layer on the adapertural face of the septum (see text-fig. 2), that the pillar zone is formed during the final stages of septum formation, at about the time of body advance and metabolic stress. Thus, the widely spaced crystalline framework of the pillar zone, as well as the open, spherulitic crystal arrays of the chalky layer may represent an effort to minimize the cost of construction of these structures, or of the time necessary for their formation, by limiting the amount of carbonate in them.

We conclude by observing that maximizing attachment strength and minimizing energetic costs are not necessarily exclusive requirements. The microarchitecture of the pillar zone may serve to optimize both. It appears to us also that Kulicki and Mutvei's (1982) reconstruction of the septal cuff in *Quenstedtoceras* is consistent with the ideas set out here, and, indeed, septal neck microstructure in many fossil cephalopods may be formulated along the lines we have suggested. It is interesting to note that if our hypotheses about pillar zone function are correct, then the fluid-transporting pillar zones of endocochliates must represent a major modification of pillar zone function present in at least some ectocochliates. Determining when in cephalopod phylogeny, and by what pathways, this shift in function took place should prove to be an exciting avenue for further research.

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