On the efficiency of the buoyancy apparatus in ammonoids: evidences from sublethal shell injuries
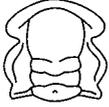
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The five greatest sublethal injuries were selected from a collection of more than 12,000 predominantly Mesozoic injured or otherwise pathological ammonoids. The loss of shell mass from these survived injuries was calculated and compared with comparable tolerances in the recent *Nautilus*. These ammonoids tolerated a shell loss up to four times greater than in *Nautilus*. The maximum tolerated shell loss indicates an unexpected buoyancy compensation mechanism. The buoyancy of the selected specimens was calculated. The results show that the buoyancy of all the observed ammonoid shells was positive. In order to maintain neutral buoyancy after injury, these ammonoids had to fill the phragmocone with a volume of mass. *Nautilus* compensated a maximum mass loss requiring a liquid refill of 3% of the cameral capacity, the ammonoids compensated a maximum of observed mass loss requiring a liquid refill of more than 10% of cameral capacity. The ratio of chamber volume/siphuncular surface area in the ammonoid *Lithacoceras* is 0.043, indicating that the relative area of the siphuncular epithelium in *Lithacoceras* is significantly higher when compared with a ratio of 0.12–0.14 in the adult *Nautilus*. The phragmocone in ammonoids offered the ability of a much more active buoyancy regulation than in *Nautilus*. □ *Ammonites, buoyancy, functional morphology, pathology, predation.*

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Every loss of shell material from the aperture of an ectocochliate owing to a predatory attack causes a mass loss. But contrary to most molluscs, the loss in mass increases the animal's last chance of escaping from its predator. The animal rises to the surface and therefore suddenly disappears beyond the view of the predator. But the mass loss also needs to be compensated for soon after the attack, otherwise the cephalopod could become trapped at the water surface and thus the victim of the predators inhabiting the air or surface waters.

This scenario is a consequence of the existence of an external buoyancy organ – the phragmocone. The phragmocone is an element of the shell of nautilids, belemnoids, ammonoids and sepiids which is partially filled with gas and maintains an approximate equilibrium between total mass and volume. The major principles of buoyancy regulation in these cephalopods have been understood since the work of Denton *et al.* (1961, 1967), Denton & Gilpin-Brown (1961a, b, 1966, 1971, 1973). The authors showed that the approximate neutral buoyancy in *Nautilus, Sepia* and *Spirula* was maintained by changing the ratio of gas and liquid in the phragmocone by osmotic pressure in the siphuncular cells. Later, Greenwald *et al.* (1982)

were able to localize an osmotic pump within the epithelial cells of the siphuncle of *Nautilus*. The siphuncular epithelial cells of the *Sepia* are similar to those of *Nautilus* (Wendling 1989). But there are some significant differences in buoyancy regulation between *Nautilus* and *Sepia*. The adult *Nautilus* is largely dry and juveniles maintained their buoyancy only by coupling shell growth with the process of emptying liquid in the phragmocone (Collins *et al.* 1980). The *Nautilus*'s short time buoyancy compensation ability is extremely restricted. Only small unexpected changes can be compensated for (Ward 1986). Normally, *Nautilus* has a slight negative buoyancy in seawater (Denton & Gilpin-Brown 1966; Ward 1987). Sepiids, in contrast, use rapid liquid emptying and refilling through their siphuncular surface to change buoyancy. *Sepia officinalis* sleeps in the daylight slightly buried into the sediment. In order to do so it needs negative buoyancy. During its active night phase, *Sepia*'s buoyancy is almost neutral, so minimizing the power which the animal needs when hovering over the sea bottom (Denton & Gilpin-Brown 1961a, b). Even if the function of the buoyancy system in *Nautilus* and *Sepia* is known for the most part, in ammonoids it is still controversial. Nothing illustrates the uncertainties
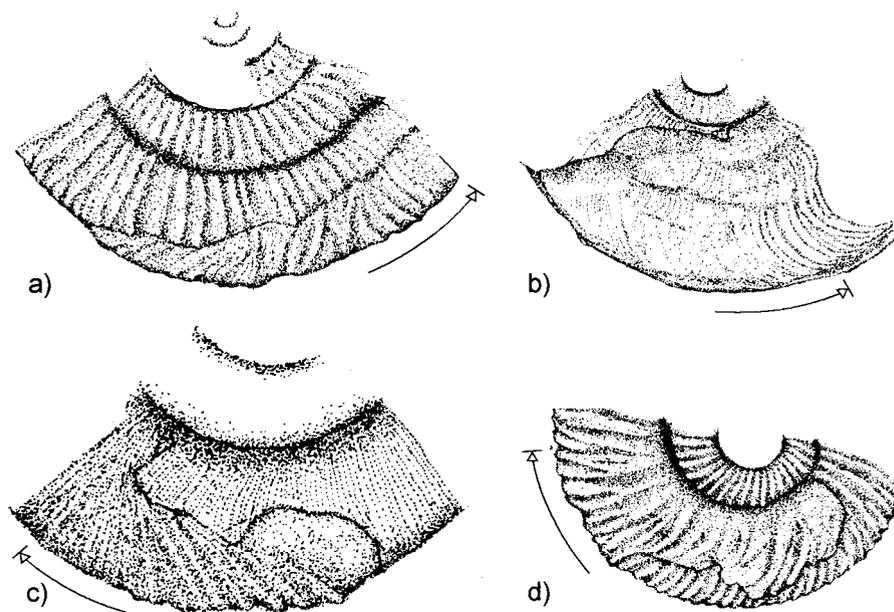
Fig. 1. Sublethal injuries observed in the current investigation. (a) *Dactylioceras commune* (PA 2182) approx. ×1. (b) *Hildoceras (Hildaites) serpentinum* (PA 10492) approx. ×1.5. (c) *Lytoceras* sp. (PA 3977) approx. ×0.5. (d) *Lithacoceras torquatiforme* (PA 10675) approx. ×0.8. The arrows indicate position of aperture at time of injury.

in this area better than the provocative article published by Seilacher & LaBarbera (1995), in which they return to the old idea of internal pressure-driven buoyancy regulation in ammonoids and therefore question the commonly held view that the total gas volume in the phragmocone is fully osmotically controlled. They assume that the last septum has a grade of flexibility which can be relaxed and contracted in order to change the volume of the gas-filled phragmocone. In 1870, W. Meigen assumed the existence of a preseptal gas chamber in *Nautilus* to explain its buoyancy regulation. Meigen believed that *Nautilus* was capable of dynamic buoyancy regulation by means of a flexible swimbladder in the deepest part of the body chamber. Later, Schmidt (1925) transferred the idea onto ammonoids. Seilacher & LaBarbera took up on the underlying principle of the model of the preseptal gas chamber to formulate its 'Cartesian diver model'. But this model conflicts with all evidence concerning muscle attachment and buoyancy calculations (for a further discussion, see Jacobs 1996). Additionally, there is controversy between Westermann (1999), Westermann & Tsujita (1999), Hewitt & Westermann (1997), Saunders (1995) and Daniel *et al.* (1997) on whether the function of the complex folded septa of the ammonoids was primarily mechanical or physiological in nature. Moreover, it is not clear what the physiological function of the folded septa was, i.e. was its purpose to aid emptying at any depth (Ward 1987), to hold a significant water-ballast (Kulicki 1979; Kulicki & Mutvei 1988; Weitschat & Bandel 1991) or was it to aid the refilling of liquid into the phragmocone (Daniel *et al.* 1997)? The discussion is based on only a few lines of evidence of the efficiency

of the ammonoid buoyancy apparatus. We still have little or no knowledge of the emptying and magnitude of liquid refilling in ammonoids.

Heptonstall (1970) suggested that the ability to compensate for an unexpected decrease in buoyancy in ammonoids was significantly higher than in the recent *Nautilus*. He computed the weight of a *syn vivo* encrustation of oysters onto the shell of *Buchiceras bilobatum* and found that *Buchiceras bilobatum* must have had one-fourth of its phragmocone volume filled with liquid, i.e. a removable ballast. Keupp & Seilacher (1999) showed a comparably high *syn vivo* encrustation of the shells by oysters and cirripedia. But Westermann's objection (1971) that the additional ballast on the ammonoid shell could have been compensated for by means of a shortening of the body chamber is still unanswered. On the other hand, Keupp (1997) illustrated Dactylioceratids with much larger regenerated shell injuries than those found in *Nautilus*, suggesting a much higher liquid refill ability in ammonoids. The aim of the current investigation is to quantify the mass loss of the greatest sublethal injuries found in ammonoids and to compare the efficiency of the buoyancy apparatus of phragmocone-bearing cephalopods. This comparison can help us to understand the basic functions of buoyancy regulation in ammonoids and in cephalopods in general.

Material

The material came from a collection of pathological ammonoids belonging to H. Keupp (Freie Universität

Table 1. Summary of the characteristics of the four observed specimens.

	Dactylioceras athleticum	*Hildoceras (Hildaites) serpentinum*	*Lytoceras* sp.	*Lithacoceras torquatiforme*
Stratigraphy	*Bifrons* zone	*Elegans* zone	Lower Cretaceous	*Planula/bimammatum* zone
Locality	Whitby/England	Altdorf/Germany	Neuchatel/Switzerland	Sacaraha/Madagascar
Preservation at time of injury:	Shell/calcitic mature	Shell/calcitic submature	Steinkern Submature	Shell/aragonitic submature

Berlin). From more than 12,000 predominantly Mesozoic individuals, most of them with sublethal injuries, the 5 specimens with the greatest observed regenerated injuries were selected (Fig. 1). Table 1 provides some information on the individuals selected. All specimens, with the exception of *Dactylioceras commune* (PA 2182), are preserved in submature ontogenetic stage. *Dactylioceras commune* represents an adult specimen with a thickened aperture and crowded last septa. All specimens are undepressed. The aragonitic shell wall was only well preserved in the case of *Lithacoceras torquatiforme* (PA 10675). In *Lytoceras* sp. (PA 3977) the shell's steinkern is preserved. The body chamber is only partly preserved in all specimens. All injuries were healed by substruction of new shell material under the rim of the breakage – a common healing pattern in all shelled molluscs (see Keupp 1998). Hölder (1973) called this kind of shell anomaly in ammonoids 'forma *substructa*'. In *H. (Hildaites) serpentinum* (PA 10492), scar-like furrows additionally mark an injury to the mantle epithelia (forma *verticata* sensu Hölder 1956). Additional specimens were used for the purpose of comparison and determination of the row data of the calculation: one *Hildoceras (H.) serpentinum* from Altorf, Germany, one *Lithacoceras torquatiforme* from Sacaraha, Madagascar, seven specimens of *Dactylioceras commune* from Whitby, England and two specimens of *Lytoceras* sp. from Haverlahwiese, Germany (Dogger).

Methods

Determination of the volume of the broken part of the shell wall

To calculate the area of the broken part of the shell, the missing original aperture was reconstructed to obtain an outline of the entire injury. If only one side of the whorl was affected by the injury (the left or right side, see Fig. 1b, d), the outline of the injury was reconstructed on the healthy side of the whorl. This was done to achieve an unaffected shell surface, because in most cases the area of the injury is bulged outward and is somewhat irregular. The surface of the broken part of the injury was digitalized in a 3D-grid by a laser reflex-microscope and later the surface area was computed using the GIS program ENTEC®. In order to calculate the volume of the shell loss, the thickness of the shell wall is also needed, but only a few of the analysed specimens had the shell walls preserved. Shell thicknesses on comparable individuals of the same taxa were therefore measured in different ontogenetic stages and in different positions on aperture (at umbilicus, flanks, venter; see Fig. 2). The mean thickness of the broken part of the shell was extrapolated by using the regression curve of the values. The surface area of the broken part of the shell multiplied by the shell wall thickness at the position of the peristome at the moment of injury gives the volume of the broken part of the shell.

Calculation of the volume of the entire shell wall

The calculation is based on an equation by Raup & Chamberlain (1967):

$$V = \frac{2}{3}\pi\left(\frac{KR_\alpha}{\ln W}\right)\left(1 - W^{-3\theta/2\pi}\right) \qquad (1)$$

Equation 1 calculates the volume of a logarithmically spired cone. The volume of the cone is given by the cross-sectional area of the aperture (K), the centre of gravity of the aperture (R_α), the whorl expansion rate (W, which is the square of the quotient of the longer half-diameter by the shorter half-diameter) and the angular length of the spiral in radians (θ). The volume of any entire shell is given by the area of aperture plus the area of the shell wall in median section. The area of the cross section of the shell wall (K shell wall) is assumed here to be the length of the outer circumference of the cross section of the whorl multiplied by the mean thickness of the shell wall. Taking into consideration the resulting error of this method (any measured circumference is an average value because of the specific variability in growth of the ammonoid and the effects of fossilization), a second error mentioned by Swan & Saunders (1987) can be neglected. Swan & Saunders (1987, appendix) used a specific adjustment factor to assess the effect of ammonoid shell coiling on
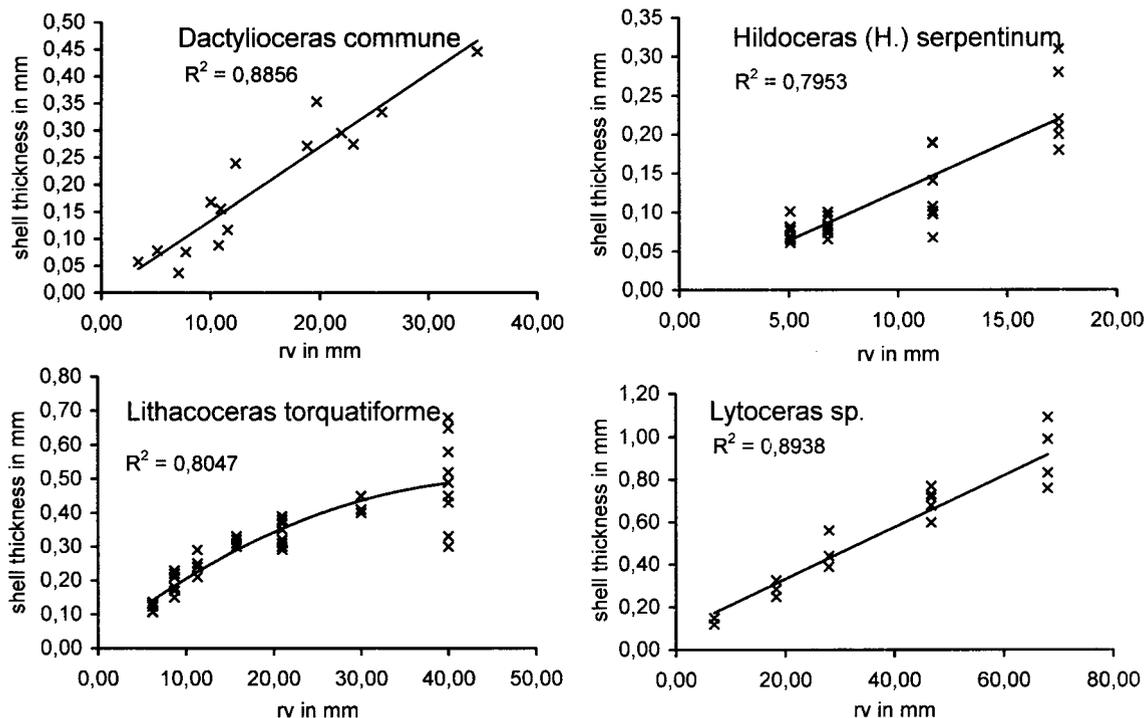
Fig. 2. Ontogeny of shell wall thickness of the four observed genera plotted against the radius between axis of coiling and venter (r_v). The plots represent measurements on single specimens in the case of *Hildoceras (H.) serpentinum*, *Lithacoceras torquatiforme* and *Lytoceras* sp. and five specimens in the case of *Dactylioceras commune*. The shell wall thickness varies around the position of the whorl. The shell wall thickness of the flanks is usually stronger than the shell wall thickness of the venter. The variance is lowest in *Lytoceras*, with a nearly circular whorl cross section, and highest in *Hildoceras*, a genus with high flanks of the whorl.

the volume of the shell wall. Additionally, the effect of sculpture must be taken into consideration. A factor is needed to model the sculpture. The sculpture elements of all ammonoids used here are ribs. Ribs can be modelled by a sinus curvature. The ratio between the length of a smooth (unribbed) curvature and a sinusoidal curvature determined by the rib height (amplitude) and rib frequency can express the factor of sculpture (F_s). The length of a sinusoidal curvature is calculated using Equation 2:

$$ls = \int_0^\theta \sqrt{1 + \left[\frac{d}{dx}ae^{-zx}\sin(bx)\right]^2}\,dx \qquad (2)$$

Where a is the average rib height (used in Equation 2 normal to r_v, the radius between the axis of coiling and venter), b is the rib frequency per whorl. The factor z is given by damping of the curvature, which is set here by the value 0.1. A source of error in this calculation results from the fact that ribbing is never exactly radial and that it does not represent an ideal sinusoidal curvature. Considering that the factor of sculpture in all ammonoids involved in this investigation only varies between 1.021 and 1.12, it will be evident that the error rate resulting from these uncertainties can be

neglected with regard to the entire shell wall volume. In addition to the volume of the outer shell wall, the volume of the septa and the siphuncle must also be taken into account. The volume of septa and siphuncle for some ammonoids was calculated by Trueman (1941) and Saunders & Shapiro (1985). The values calculated by Saunders & Shapiro (1985) on Paleozoic genera vary between 5% and 14.6% of the volume of the entire shell wall. The values calculated by Trueman (1941) on Mesozoic genera are lower (between 3% and 5.7%). The current calculation is based on a value of 5.7% as the mean of the values of both investigations. To calculate the volume of the entire shell wall, the volume of the outer shell wall must be corrected by these values using a factor (septal factor) of 1.06.

The variables needed for the calculation are easy to measure directly or by sectioning the specimen in a direction perpendicular to the median plane. The cross-sectional areas of the whorl (K) were measured at different ontogenetical stages and plotted (Fig. 3) after sectioning off four not-injured and well-preserved specimens by the same taxa. The resulting regression curve of the measured values was used to extrapolate K at the position of the peristome at the moment of injury. R_α was calculated graphically by drawing the cross-sectional areas on a grid and
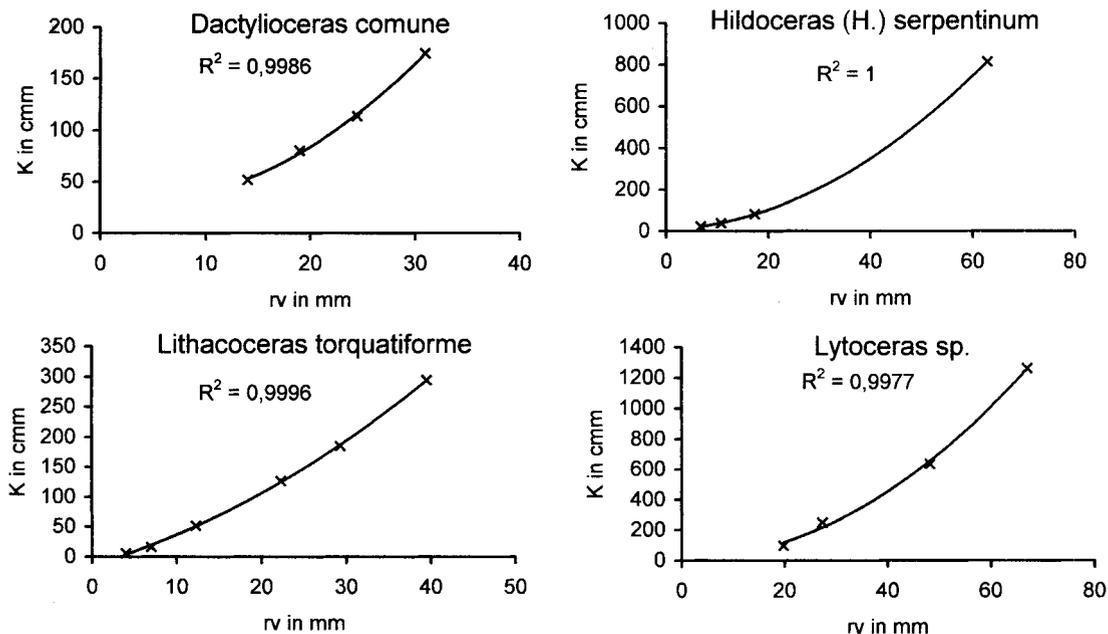
Fig. 3. Ontogeny of the area of cross section of the four observed genera plotted against the radius between axis of coiling and venter (r_v). The plots represents measurements on single specimens.

measuring the distance of the centre of gravity from the ventral side of the aperture. The ratio between the distance of the centre of gravity from the venter and the corresponding r_v is used to calculate R_α at the position of the peristome at the moment of injury. The cross-sectional area of the shell wall is calculated by multiplying the mean value of shell thickness at the position of the peristome at the moment of injury with the outer circumference of the cross section of the aperture (excluding the umbilical surface). W was measured at the position of the peristome at the moment of injury by using the formula given above.

Buoyancy determination

The maximal theoretical buoyancy of the ammonoid is provided by the mass of the displaced seawater minus the sum of the mass of the shell wall, the dry cameral membranes, the aptycha (if existing) and the soft body. Assuming the ammonoids lived in near-neutral buoyancy, the difference between calculated buoyancy and neutral buoyancy shows the mass of the liquid that occupied the chambers (fill fraction). It should be noted that the term fill fraction, which comprises all chambers of the phragmocone as used here, is different from the original use of the term by Hewitt & Westermann (1996), who distinguish between the fill fraction of the last chamber and a dynamic fill fraction, which excludes the most recently built chamber.

The *mass of the displaced seawater* is calculated by

inserting the values of the cross-sectional area of the aperture at the position of the peristome at the moment of injury (K aperture) plus the cross-sectional area of the shell wall at the aperture (K shell wall), R_α and θ at the position of the peristome at the moment of injury (which can all be extrapolated by the regression curve, see Fig. 3) in Equation 1. The result of these calculations provides the volume of the entire ammonoid based on the assumption that the whole body chamber is occupied by the soft body.

The *mass of the entire shell wall* is calculated based on an assumed density of the shell material of 2.62 g/ml (the density of the shell of *Nautilus* is 2.62 g/cm^3, according to Rayment 1958 and Saunders & Shapiro 1986) or, alternatively, 2.69 g/ml (the value for uniform nacre given by Hewitt & Westermann 1996; Hewitt *et al.* 1999).

The *mass of the soft body* is calculated based on the assumption that the volume of the soft body equals the volume of the body chamber (which is surely too high, but is used for want of any data on the expansion of the soft body in the body chamber). The volume of the body chamber equals the volume of the displaced seawater minus the volume of the entire shell wall and the phragmocone lumen (inclusive volume of cameral membranes). The volume of the body chamber is dependent on the position of the last septum. The current calculation uses averaged data from several sources (Diener 1916; Trueman 1941; and own measurements on comparable specimens) for want of own data. Use of averaged values of body chamber

Table 2. Masses (M, in g), volumes (V, in ml) and specific densities (δ_{spec}, in g/ml if seawater density is 1.026, density of the shell material is 2.69 g/ml and no water, except the capillary trapped water of the cameral membranes, fills the phragmocone lumen) of four modelled ammonoids calculated from raw data (r_v, radius from spiral axis to venter at the position of the peristome at the moment of injury; BCL, length of the body chamber in degrees; W, whorl expansion rate *sensu* Raup & Chamberlain, 1967; K aperture, cross-sectional area of the whorl at r_v; K shell wall, cross-sectional area of the shell wall at r_v; K phragmocone, cross-sectional area at position of the last septum; R_α aperture, radius from spiral axis to centre of gravity of K at r_v; R_α phragmocone, radius from spiral axis to centre of gravity of K at position of the last septum; F_s, factor of sculpture, see text for explanation). The fill fraction gives the volume of liquid contained in the lumen of the phragmocone (cc, cameral capacity, if the volume of the cameral membranes is excluded) under the assumption of neutral buoyancy and of seawater density of 1.026 g/ml. Three different values of fill fraction are determined: The fill fraction at a density of the shelly matter of 2.69 g/ml or alternatively 2.62 g/ml and the fill fraction under the assumption that the chambers contain no significant cameral membranes. For a full explanation of the calculation see text.

	D. commune	H. (H.) serpentinum	L. torquatiforme	Lytoceras sp.
r_v	44.8	38	32	63
BCL	390	260	390	270
W	1.60	2.11	1.85	1.96
θ	12π	8π	10π	10π
K aperture	294	331	218	1113
K shell wall	29.3	30.6	16.9	88.7
K phragmocone	136	144	93.7	412
R_α aperture	36.1	23.1	28	42.9
R_α phragmocone	21.73	13.5	14.5	25.2
F_s	1.12	1.04	1.09	1.02
V entire ammonoid	47.250	21.480	21.140	148.600
V shell wall, without sculpture, excl. septa and siphuncle	4.710	1.990	1.640	11.840
V entire phragmocone	13.130	5.449	4.717	32.330
V chamber lumen (~capacity. cc)	11.292	4.686	4.057	27.800
V_{intern} body chamber	34.120	16.031	16.000	116.270
M shell wall ($\delta = 2.62$), sculptured excl. septa and siphuncle	13.82	5.40	4.69	31.67
M shell wall ($\delta = 2.69$), sculptured	14.19	5.55	4.81	32.52
M septa and siphuncle ($\delta = 2.62$)	0.93	0.34	0.31	1.94
M septa and siphuncle ($\delta = 2.69$)	0.95	0.34	0.32	1.99
M cameral membranes	1.9	0.81	0.69	4.78
M aptychus		0.27	0.18	
M soft body	35.99	16.91	17.33	122.66
M diplaced water	53.31	24.08	23.37	164.61
M entire ammonoid ($\delta = 2.62$)	52.68	23.76	23.20	161.05
M entire ammonoid ($\delta = 2.69$)	53.08	23.88	23.33	161.95
Fill fraction ($\delta = 2.62$) in % cc	5.4	7.3	4.1	12.5
Fill fraction ($\delta = 2.69$) in % cc	2	4.1	0.9	9.3
Fill fraction ($\delta = 2.69$) in % cc excl. cameral membranes	13	14.8	12	19.4
δ_{spec} entire ammonoid excl. fill fraction, ($\delta = 2.69$)	0.96	0.96	0.97	0.95

length is by no means the greatest source of error in the current calculation (see discussion below). The density of the soft body of *Nautilus* is given by Ward (1986) as being between 1.026 g/cm^3 (coelomic fluid) and 1.068 g/cm^3. Hewitt *et al.* (1999) calculated in buoyancy calculations of belemnites with a soft body density of 1.05 g/cm^3, and Saunders & Shapiro (1986) calculated with a soft body density of 1.055 g/cm^3 for ammonoids. The figure provided by Saunders & Shapiro (1986) meets the average mean of all the given densities and is therefore used in this investigation. The volume of the body chamber is calculated by the volume of the entire ammonoid (see above) minus the volume of the cylinder at the position of the last septum (which may be called the volume of the phragmocone). The volume of the phragmocone is given by K, R_α and θ at the position of the last septum, which can be extrapolated again by the regression curve (see above).

It should not be confused with the *cameral capacity*, which is the phragmocone volume minus the volume of septa and siphuncle and the volume of the cameral membranes. The term was introduced by Hewitt & Westermann (1996) to specify the volume of the lumen of the phragmocone.

The *mass of the cameral membranes* is determined based on the assumption that the membranes occupied approximately 14% of the cameral space (Hewitt & Westermann 1996). The density of the cameral membranes, which are thought to be saturated with cameral liquid, is assumed to be the same as the density of the soft body (Hewitt pers. comm.).

Account had to be taken of the *mass of the aptychi* of *Lithacoceras* and *Hildoceras*. The lower jaws of *Hildoceras* are calcified and known as *Cornaptychus*. Lower calcified jaws of Perisphinctides are known of (Keupp 2000), but to my knowledge not reported for *Lithacoceras*. Nevertheless, the current calculation takes the mass of the aptychi of both genera into consideration. According to Hewitt & Westermann

Table 3. Volumes (V, in ml) and masses (M, in g) of the injured ammonoids under the assumption of a density of shell material of 2.69 g/ml. The fill fraction gives the volume of liquid contained in the chamber lumen (cc if the volume of the cameral membranes is excluded) under the assumption of balanced buoyancy. The sudden buoyancy loss because of the predation is compensated for by a liquid refill which is given here as percentage of the chamber capacity or alternatively as the percentage of the volume of the phragmocone lumen without cameral membranes. The relative shell loss due to predation is given as a percentage of the mass/volume of the entire shell wall inclusive septa and siphuncle.

	D. commune	*H. (H.) serpentinum*	*L. torquatiforme*	*Lytoceras* sp.
V broken shell part	0.619	0.401	0.443	2.835
V injured shell	5.629	2.190	1.908	12.823
M broken shell part ($\delta = 2.69$)	1.67	1.08	1.19	7.63
M displaced by the injured ammonoid	52.68	23.67	22.91	161.7
M of the injured ammonoid ($\delta = 2.69$)	51.41	22.80	22.14	154.3
Fill fraction in % cc of injured spec. ($\delta = 2.69$)	10.89	18	18.57	25.86
Fill fraction in % of injured spec excl. cameral membranes ($\delta = 2.69$)	20.84	27.03	27.58	33.93
Refilling in % of cc	8.9	13.9	17.7	16.5
Refilling in % of cc excl. cameral membranes	7.9	12	15.6	14.6
Shell loss in % of shell wall incl. siphuncle and septa)	10.1	18.3	23.2	22.1

(1993), the average original density of a *Leavaptychus* is 1.655 g/ml. It is assumed that the volume of the aptychus equals the cross-sectional area of the aperture with a thickness identical to the shell wall thickness.

Results

The raw data and the results of the calculation are given in Table 2. In order to interpret the results of the calculation, the extent of its inherent error must be discussed, i.e. the error regarding measurement of the length of the body chamber, the cross-sectional area of the shell wall, adult modifications in body chamber shape and length, as well as shell wall thickness, dorsal shell layers, individual modifications and irregularities of the sculpture, constrictions, ontogenetical changes in W, etc. The major error in the current calculation results from the use of average (*Lytoceras* sp.) or maximum values of body chamber length (*Dactylioceras, Hildoceras, Lithacoceras*). Just a few degrees of change in the length of the body chamber can alter the entire density of the ammonoid dramatically. But the body chambers of ammonoids are seldom fully preserved. Consequently the determination of buoyancy of ammonoids is more or less a theoretical project if no exact values of the individual body chamber length of the specimen are available. The averaged body chamber length of a genus or species is only of theoretical importance. Diener (1916) noticed that in *Dactylioceras commune* strong changes between individual specimens can be found and that the intraspecific variance can be great in *Lytoceras*, as it is in most genera. Westermann (1971) emphasized that ontogenetic changes in the length and shape of

body chamber are normal in ammonoids, as with *Nautilus*. The inaccurate values for body chamber length at time of injury of the observed specimens strongly limit the use of the current calculation and may be the reason for the high density values of *Dactylioceras commune* and *Lithacoceras torquatiforme*. Nevertheless, they did not affect the values of shell wall mass significantly. But there are uncertainties in the determination of the mass of the shell wall too. *Dactylioceras* and *Lytoceras* developed a dorsal shell wall of uncertain thickness and with an unquantified expansion. *Dactylioceras* built an entire second shell wall underneath the outer shell and the prismatic layer of that second shell wall lined the entire inside of the shell and bridges across the ribs (Howarth 1975). Although these shell layers are comprised in the thickness measurement of Fig. 2 they must have slightly affected the volume of the phragmocone lumen. This effect is not considered in the current calculation. The mature *Dactylioceras* developed an apertural thickening, the mass of which is unquantified. But its mature thickening is probably linked with the shortening of the body chamber (Westermann 1971) to offset the mass increase. The shell of any juvenile ammonoid wedges out towards the peristome to some degree, which is not considered here. In addition to these sources of error, the current calculation contains a methodical error. Swan & Saunders (1987) noticed that a unit of shell cross area nearer the umbilicus contributes less to the volume than a unit of shell cross area nearer the venter. They adjust their calculations by a factor for shell thickness ratio. But in the light of the uncertainties of the raw data of the calculation, neither of these errors seems to be relevant for the current calculation, nor does the inaccurate density of the shell matter play any significant role. The weight of the entire ammo-

Table 4. Comparison of the tolerance of a sudden buoyancy increase in ammonoids, *Nautilus* and *Sepia*. In *Nautilus* the shell loss due to predation is strongly limited. *A sudden buoyancy increase higher than 5% of the total shell mass is not tolerated in *Nautilus macromphalus* (Ward 1986). The buoyancy increase in *Nautilus* is compensated by a liquid refill of maximum 3% of the volume of the chamber lumen Ward (1987). °Denton & Gilpin Brown (1961b) indicated the daily rhythm of the density of the cuttlebone of *Sepia officinalis*, which is maintained by a compensatory liquid change of about 6% of the chamber capacity (Denton & Gilpin Brown 1973). There is no catastrophic scenario that would produce a sudden buoyancy increase in *Sepia*, but it can be expected that the compensatory liquid refill will be higher than 6% of the chamber capacity. The capability of compensation of catastrophic mass loss in ammonoids seems significantly higher than in *Nautilus*.

Genus	Tolerated shell loss in % of the shell wall, incl. septa and siphuncle	Compensatory liquid refill in % chamber capacity
Dactylioceras	10	9
Hildoceras (H.)	18	14
Lithococeras	23	18
Lytoceras	22	17
*Nautilus**	5	3
Sepia°	–	>6

noid with a shell density of 2.62 g/ml differs from an identical ammonoid with a shell density of 2.69 g/ml by 7%. In summary, it should be noted that the results presented here can give only approximate values for the chamber capacity, but the values of shell mass and volume are closer to reality. The error is estimated to be no more than 10% plus the variance because of the two density values. An error of 10% in values of the shell mass leads to a 1% error in the calculated relative shell loss. It follows that calculation of the tolerated shell loss, given in percent of the entire shell in Tables 3 and 4, is only slightly too high. Comparison of the results of the calculation with published data by Ward (1986, 1987) on *Nautilus* and by Denton & Gilpin Brown (1973) on *Sepia* in Table 4 shows that the tolerated shell loss in ammonoids is significantly higher than in *Nautilus*. If a mass loss after a failed predatory attack was assumed to be compensated for, as in *Nautilus* (Ward 1986), by a liquid refill, this refill can be compared by the percentage of chamber capacity occupied by the refilled liquid. In comparing, it will be evident that liquid refill ability in ammonoids, which was more than 10% of chamber capacity, was significantly higher than observed in recent *Nautilus* by Ward (1986) (no more than 3% of chamber capacity). *Sepia* changes its buoyancy dependent on its mode of activity (night/day rhythm). By doing so, *Sepia officinalis* periodically emptied and refilled liquid to a volume of 6% of the phragmocone (Denton & Gilpin Brown 1961b, 1973). Because there is no scenario in which a catastrophic mass loss in

living sepia could be caused, its maximum liquid refill ability is unknown. But it seems that liquid refill ability in ammonoids is closer to the tolerance of *Sepia* than that of *Nautilus*.

Discussion

The observed ammonoids survived a predatory attack and the loss of a large part of their shell, suddenly rose to the surface and compensated for mass loss quickly. There is no other mechanism of compensation conceivable than the refilling of liquid into the chambers of the phragmocone at the water's surface. Experimental observations made by Ward & Greenwald (1981) and Ward (1986) produced some results on refilling rates, osmolality of the refilled liquid and the amount of maximum refill in *Nautilus*. One of their unexpected results was finding a limit to refilling in *Nautilus* at approximately 3% of the chamber volume (Ward 1986). How refilling occurred and the reason for its limiting remain obscure. Ward (1987) noted that refilling could be a product of blood pressure within the siphuncular strand. Bandel & Spaeth (1983) have suggested that refilling is limited by the inherent gas pressure of the chambers, which is slightly lower than atmospheric pressure (Denton & Gilpin-Brown 1966). Any liquid refill in the chambers will compress the contained gas. In ammonoids, the maximum refill is 9–18% (see Table 3), which is significantly higher than in *Nautilus*. This high ability of refill in ammonoids may be explained either by higher blood pressure in the siphuncle of the ammonoids or by lower gas pressure in the ammonoid chambers. Neither of these explanations seems very likely and there is no evidence to substantiate them. The most obvious difference between the architecture of the phragmocone of *Nautilus* and that of the ammonoids is the folded ammonoid septa. As in *Nautilus*, the septal faces and the inner shell wall of ammonoids are lined by organic membranes (Weitschat & Bandel 1991). These membranes, the pellicle, are well observed in *Nautilus*. The pellicle is a porous sheet consisting of numerous interwoven organic fibres (Ward 1987; Grégoire 1987). It contains significant volumes of liquid and has a 'mucus-like appearance in freshly broken shells' (Ward 1987, p. 40). Because of its hydrophilic quality, the pellicle plays an important part in the transportation of fluid in the chambers and for small-scale buoyancy changes. In partially emptied chambers, the pellicle works like blotting paper to transport the liquid to the siphuncle (Ward 1987, fig. 2.3). The forces that act in blotting paper are capillary forces. Capillary forces are directed

forces at the surface of different phases e.g. liquid, conchiolin and chamber gas. They depend, according to the law of Fick, on the surface tension of the liquid and the diameter of the capillary. If the adhesion in the liquid is greater than the cohesion to the solid surface, as in the case of the chamber liquid, the capillary forces cause capillary pressure against the gas pressure. Refloatation experiments of dry *Nautilus pompilius* shells of Hewitt & Westermann (1996) demonstrate the effect of the capillary forces in the siphuncular tube wall and the pellicle. The weight of a dry shell of *Nautilus* dipped in water increases rapidly at the initial moment because of the liquid refill by capillary forces which are activated in the siphuncular tube wall and the pellicle. It is obvious that the greater the volume of the capillary tissue the greater the ability of capillary fluid transport and the greater the ability of liquid storage. The pellicle, which lined the inner surface of the ammonoid chamber, is significantly greater than that of *Nautilus* and consequently greater than the ability of ammonoids to store liquid in the pellicle. Additionally, the chambers of the ammonoids were divided by a system of numerous intracameral conchiolin and protein layers (Weitschat & Bandel 1991; Hewitt *et al.* 1991; Checa 1996; Mapes *et al.* 1999). Checa (1996) distinguishes between three types of sheets: membranes replicated by the rear mantle, sequentially secreted membranes and membranes produced by desiccation of the cameral liquid. Checa assumed that the membrane secreted by the rear body 'was related to a more efficient transport'. In the current calculation, it is assumed *sensu* Hewitt & Westermann (1996) that the total volume of the pellicle and the sheets is 14% of the cameral lumen, and that they stored a significant volume of liquid (see difference of fill fraction of chambers with cameral membranes/without cameral membranes in Table 2). If the chambers were partially filled with gas the intracameral sheets, as well as the complex folded septa, subdivided the remaining cameral liquid into small compartments between narrow nooks. The lower radii of these liquid reservoirs provide, according to the law of Fick, higher capillary forces. Kulicki (1979), Weitschat & Bandel (1991) and Checa (1996) paid attention to this effect on the ability of liquid storage in ammonoids. Daniel *et al.* (1997) deduced that this phenomenon affected refilling ability and consequently the tolerance of sudden shell loss due to predators. Independently of the controversial debate on the mechanical function of the septa, the current calculation supports this idea. The ammonoids tolerated a significantly higher shell loss than *Nautilus*. The compensation of sudden shell loss is also a function of time. The injured ammonoid had to compensate the weight loss quickly. Measurements of the passive flow

of liquid through the siphonal tube carried out by Chamberlain (1978) and Chamberlain & Moore (1982) suggest that the permeability coefficient of the tube of *Nautilus* (~24 µd: Chamberlain 1978) is about three orders of magnitude greater than the rates of osmotic flow in living animals (Chamberlain & Moore 1982). Consequently, the transport capacity of the siphonal tube is not a limiting factor for short-time buoyancy compensation ability. Ward (1982) showed that in *Nautilus* the liquid removal rates are dependent on the relative surface area of the siphuncular epithelium. Because there are no substantial differences in all known cephalopod siphuncular epithelia (see, e.g., Tanabe *et al.* 2000), the ratio between the chamber volume and the siphuncular area should be a measure of short-time buoyancy change ability. In a *Lithacoceras* with r_v of 36.5 mm, K phragmocone of 254.2 and a siphuncular diameter of 1.1 mm, the ratio between chamber volume in ml and siphuncular surface area in mm^2 is 0.043. The chamber volume/siphuncular area ratio in the adult *Spirula* is 0.13 and Ward (1982) provides a ratio of approximately 0.12–0.14 for the adult *Nautilus*. The ratios of some other cephalopods are also plotted in Ward (1982, fig. 6). In comparison to these ratios, it will be evident that the relative siphuncular surface area of *Lithacoceras* has a dimension more like that of Orthocerids such as *Bifoveoceras* or *Michelinoceras* than of modern cephalopods like *Nautilus* or *Spirula*. We should therefore expect higher active and fast buoyancy regulation ability in ammonoids than in *Nautilus* and *Spirula*. But the relative siphuncle area is much smaller than that of *Sepia* given by Ward (1982), who has a ratio of approximately 0.01. Because there is no measure to estimate the ability for diurnal buoyancy changes it will be difficult to interpret these ratios. In summary, it will be evident that the tolerated sudden shell loss owing to injury in the observed ammonoids indicates a high ability to compensate for sudden buoyancy decreases. Evidence of the morphology of the ammonoid phragmocone is consistent with the suggestion that an active buoyancy regulation mechanism existed in ammonoids. But it is not clear if ammonoids were capable of diurnal buoyancy regulation as in the case of *Sepia*.

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