New look at ammonoid taphonomy, based on field experiments with modern chambered nautilus

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ABSTRACT

Field experiments with *Nautilus pompilius* in the Philippines have uncovered two previously unknown postmortem phenomena: (1) waterlogging of the phragmocone does not occur until the mantle tissue detaches from the shell due to decomposition, and (2) the phragmocones of empty shells flood with seawater rapidly due to low internal gas pressure (<0.9 atm). The latter is more significant for small shells, because of the lower total gas pressure in their phragmocones compared to larger shells, and the smaller limit of seawater volume that still allows flotation. The limiting diameter for shells to sink from only the latter mechanism (lower internal gas pressure) is ~200 mm. Ammonoids generally have body chambers longer than *N. pompilius*, but the ratio of body chamber volume to phragmocone volume for most ammonoids is the same as for *N. pompilius*. This ratio is the determining factor that allowed ammonoid shells either to float or sink from pressure compensation alone. This strongly suggests that (1) their limiting shell diameters approximate that of *N. pompilius* (i.e., ~200 mm), (2) such shells sank rapidly close to their habitats, even if they initially floated, and (3) only large shells had the potential to drift postmortem over long distances. These findings are crucial to interpreting the early taphonomic history of extinct ammonoids.

Keywords: ammonoids, cephalopods, experimental investigations, *Nautilus*, taphonomy.

INTRODUCTION

Ammonoids, an extinct group of Cephalopoda, have been interpreted as being either nektobenthic or nektoplanktic organisms (Saunders and Shapiro, 1986; Jacobs and Chamberlain, 1996). An understanding of their taphonomic history is crucial for accurately deciphering their life history. In particular, postmortem shell dispersal over long distances frequently has been called upon in studies of ammonoid taphonomy. Such previous studies have been based on the physical attributes of fossil shells (e.g., functional morphology, the presence of epizoans, and predatory signatures) and extrapolation from modern nautiluses (e.g., Reyment, 1973; Chamberlain et al., 1981; Mapes and Chaffin, 2003; Maeda et al., 2003). The study of Denton and Gilpin-Brown (1966) on the emptying mechanism of *Nautilus* and subsequent studies on buoyancy control are fundamental to understanding the paleobiology and taphonomy of ammonoids (see Greenwald and Ward, 1987; Jacobs and Chamberlain, 1996). The key assumptions in previous studies of ammonoid taphonomy were: (1) the animals were neutrally buoyant or slightly heavier than seawater during life, (2) seawater began to flood the phragmocone (gas-filled chambers) through the siphuncle immediately after the animal's death, and (3) dead shells that ini-

tially floated at the sea surface never sank to the bottom afterward, unless the phragmocone was severely damaged and/or covered by heavy epizoans, and may have drifted thousands of kilometers as the phragmocone acted as a sealed vessel (House, 1987, and references therein). Although the presence of neutral to slightly negative buoyancy is well recognized (see Greenwald and Ward, 1987), the timing of waterlogging has not been rigorously studied, and floating duration has been reported only anecdotally, except for one probable drift of 138 d for more than 1000 km, from Palau to Mindanao in the Philippines (Saunders and Spinosa, 1979).

Here we report two previously unknown postmortem phenomena in *Nautilus pompilius*, based on field experiments in the Philippines. Our results contradict previous interpretations, and therefore shed new light on the understanding of the early taphonomic history of modern nautiluses, as well as extinct ammonoids.

MATERIAL

All specimens of *N. pompilius* used in our experiments were collected alive by local fishermen with fishing traps at depths of ~200 m off the coast of Tagnan, Panglao Island, in Bohol Province of the Philippines (see Wani, 2004, their Fig. 1).

RATE OF WATERLOGGING

Method

We observed the onset and progress of waterlogging and the condition of the soft body for 26 specimens of *N. pompilius* by setting them at two different depths around Balicasag islet off Panglao Island in May–June 2003: 18 specimens (72–195 mm in shell diameter) on a bottom ~320 m deep (seawater temperature was 12.2 °C during the experiment); and 8 specimens (124–177 mm in shell diameter) on a bottom ~50 m deep (seawater temperature was 26.8 °C during the experiment). Before setting out the specimens, the fresh dead animals were wrapped in fine nylon mesh bags (1 mm mesh) and then enclosed in plastic mesh boxes (200 × 200 × 250 mm), in order to protect the animals from attacks by scavengers. These animals were retrieved after 1 d (1 specimen), 4 d (4 specimens), 7 d (10 specimens), and 14 d (4 specimens). We observed the condition of the soft bodies and examined all specimens, whether or not the phragmocone was filled with seawater.

Results and Discussion

Table 1 shows our results regarding the presence or absence of seawater in the phragmocone, the condition of the mantle attachment to the inner shell surface of the body chamber, and other observations. We observed that: (1) waterlogging did not occur after 1 d of immersion in any specimen at either depth; (2) most specimens at the shallow depth (~50 m) were waterlogged within 3 d; (3) all the specimens at the shallow depth produced a large amount of putrefactive gas within 3 d; (4) most specimens >157 mm in shell diameter were waterlogged within 7 d at the greater depth; and (5) the phragmocones of specimens <100 mm in shell diameter were still empty of water even after 14 d at the greater depth. In all waterlogged specimens, the mantle tissue was detached from the shell at the dorsal portion near the umbilicus.

Our results clearly contradict the previous view that waterlogging in *N. pompilius* occurs immediately after death, and show that the time lag between death and waterlogging is quite long and probably depends on animal size and decomposition state (the latter also depending largely on seawater temperature).
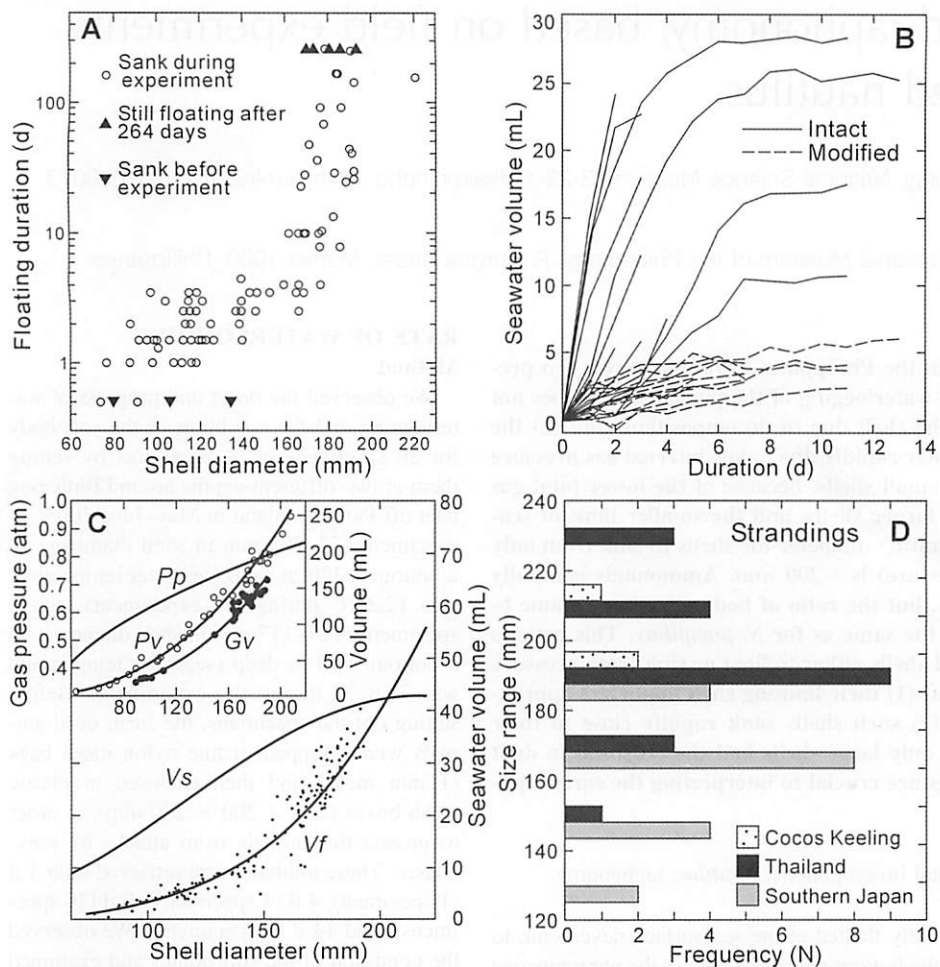
Figure 1. Results of experiments on shell floating duration in *Nautilus pompilius*. A: Floating duration of 87 empty shells. B: Comparison of waterlogging rate between 15 intact and 13 modified shells (last 10 chambers were drilled and sealed with epoxy resin), using empty shells of animals captured alive (t-test for mean seawater volume of two shell groups, $p < 0.01$ for first day and $p < 0.005$ after second day). C: Five curves show gas pressure and volume changes. *Pv*—volume of phragmocone; *Gv*—total gas volume of phragmocone under 1 atm pressure in live-captured animals; *Pp*—total gas pressure of phragmocone in live-captured animals, $Pp = Gv/Pv$; *Vf*—limit of seawater volume in phragmocone that still allows flotation, determined by adding weights to floating shells; *Vs*—seawater volume needed for pressure compensation, $Vs = Pv - Gv$. D: Size distribution of stranded *N. pompilius* shells.

These results suggest that waterlogging is triggered by disintegration of the mantle attachment, particularly on the dorsal portion of the soft body near the umbilicus. This mechanism is particularly conspicuous on larger animals, which implies that the relatively greater body weight of larger animals pulls the mantle attachment apart faster than in smaller animals. This apparently reflects the fact that weight increases in three dimensions, whereas the area of mantle attachment increases in just two dimensions. The soft bodies of modern nautiluses have an annular mantle attachment at the rear of the body chamber, which consists of a pair of large, tightly fused retractor muscles, and a rather weakly fused myoadhesive attachment (Isaji et al., 2002, and references therein). These extend around the mantle so as to completely block the rear side of the mantle from seawater. To confirm the deterioration of this muscle attachment as the cause of waterlogging, we artificially removed part of the annular attachment from the shell, connected a pressure gauge to one chamber of the phragmocone, and gradually brought it down to a depth of 30 m by scuba diving. The results show that seawater entered the phragmocone proportionate to the increase in water depth, which clearly indicates that the detachment of the mantle from the shell triggered waterlogging of the phragmocone.

These findings also provide new insights into nautiloid biology. Previous studies hypothesized that ambient pressure resulted in waterlogging of the phragmocone through the siphuncle in life, and therefore that osmotic pumping worked continuously to keep the chambers of the living shell empty of liquid (Greenwald and Ward, 1987, and references therein). However, our findings clearly show that waterlogging does not occur, even at depth, unless muscles are detached from the shell's interior surface. This implies that the shell interiors were not subject to water pressure in life, and therefore nautiluses used less energy to maintain buoyancy than previously thought. The pressure within the siphuncular tissue is the same as ambient water pressure, and the siphuncular tube is structurally permeable to liquids (Denton and Gilpin-Brown, 1966; Collins and Minton, 1967). Thus, we infer that the siphuncular tissue-tube complex, regardless of cause, protects against waterlogging of the phragmocone.

SHELL FLOAT TIMES
Method

We recorded the floating duration of *N. pompilius* by putting 87 empty shells (74–220 mm in diameter), immediately after the removal of the soft body parts, into two floating cages (1 × 1 × 0.5 m) in the sea off Balicasag

TABLE 1. RESULTS OF EXPERIMENTS ON WATERLOGGING RATE

Duration (d)	No. of specimen	Water-logging	Mantle contact	Posterior mantle tissue	Viscera	Pigment in hood
At bottom ~320 m in depth (>157 mm in diameter)						
4	1	None	Attached	Complete	Intact	Present
7	8	Present	Detached	Complete	Partly dissolved	Absent
14	2	Present	Detached	Complete	Partly dissolved	Absent
At bottom ~320 m in depth (<100 mm in diameter)						
4	3	None	Attached	Complete	Intact	Present
7	2	None	Attached	Complete	Intact	Absent
14	2	None	Attached	Complete	Partly dissolved	Absent
At bottom ~50 m in depth (124–177 mm in diameter)						
1	1	None	Attached	Complete	Intact	Present
3	7	Present	Detached	Torn*	Partly dissolved	Absent

*A great volume of putrefactive gas was generated.

in 1999–2001. We omitted all shells that sank due to breakage from hitting other individuals and/or the cage frames. In order to recover the complete volume of the phragmocone (Pv), we crushed additional long-preserved, empty shells of various sizes (with pressure inside and outside the phragmocone being the same, as determined with a pressure gauge) with pliers, and collected the gas underwater into a water-filled graduated cylinder. We then raised the cylinder until the water level in the cylinder was even with the water surface in the water tank we used, so that the gas in the cylinder was normalized to atmospheric pressure. The gas pressure in the complete phragmocones of live animals (Pp) was calculated as follows. The gas volume (Gv) was measured by the same method noted above, using fresh shells. Because the internal gas pressure was <1 atm, the internal gas volume recovered was smaller than if it had been at 1 atm. We generated a Pv curve from 34 specimens and a Gv curve from 17 specimens, from which a Pp curve was obtained using the formula $Pp = Gv/Pv$.

Results and Discussion

Our experiment demonstrates that floating duration is size dependent (Fig. 1A): (1) 55 shells with diameters of <170 mm sank in <10 d (3.5 d on average), except for one shell; (2) 24 shells with diameters of >170 mm floated for 4–264 d; (3) 5 shells with diameters of >170 mm continued to float after 264 d; and (4) 3 shells with diameters of <135 mm failed to float, owing to the presence of cameral liquid within the phragmocone chambers.

We interpret shell sinking as the result of seawater intake through the siphuncle tube, to compensate for the low gas pressure in the phragmocone. Gas pressure in a newly formed chamber is considerably lower than 1 atm, due to the osmotic removal of cameral liquid, and it is lowest in the final chamber and increases in earlier ones due to simple gas diffusion, but never exceeds 1 atm (Denton and Gilpin-Brown, 1966; observations herein). To test this hypothesis, we compared waterlogging rates between 15 intact and 13 artificially pressure-released shells (in which the last 10 chambers were drilled and then sealed with epoxy resin). Intact shells had a much higher waterlogging rate than pressure-released shells (Fig. 1B).

We observed that the total gas pressure in a phragmocone (Pp) increases with growth (i.e., approaching ~0.9 atm; see also Denton and Gilpin-Brown, 1966), and that the volume of seawater taken in due to pressure compensation (Vs) increases at a rate much slower than the increasing rate of the volume limit

for flotation (Vf) (Fig. 1C). This implies that smaller shells take in seawater to exceed the volume limit for flotation (Vf) faster than do larger shells. As a consequence, smaller shells sink faster, larger shells float longer, and shells $>\sim200$ mm never sink from this mechanism alone. Our findings suggest that most shells sink relatively rapidly and that only large shells have the potential to drift postmortem over great distances.

Our model explains, for the first time, why stranded shells on Ko Phe Tra (Andaman Sea) and Cocos Keeling (Indian Ocean), more than 2000 km from the nearest *N. pompilius* habitat, are mostly >180 mm in diameter (Fig. 1D). In contrast, dead shells that drifted ashore in southern Japan are dominantly <180 mm in diameter, although they are thought to have drifted 1000 km from the Philippines (House, 1987). However, live-capture records in southern Japan (Hamada et al., 1980) suggest that such drift shells are derived from either temporary or permanent populations in less-distant areas.

IMPLICATIONS FOR AMMONOID TAPHONOMY

The postmortem scenario for ammonoids most likely involved many factors, such as habitat depth, water temperature, animal size, shell structure, and the presence or absence of agents that resulted in sudden loss of the soft body. Except for shell structure and animal size, these factors are poorly known. In particular, the habitat depths of ammonoids have long been debated (e.g., Kase et al., 1994; Seilacher and LaBarbera, 1995; Westermann, 1996; Moriya et al., 2003). However, ammonoids had siphuncular and muscular systems, irrespective of shell form, and a marginally more complicatedly fluted septal wall, similar to modern nautiluses (e.g., Doguzhaeva and Mutvei, 1991, 1996; Kulicki, 1996; Tanabe et al., 2000), suggesting that they had similar buoyancy regulation mechanisms and postmortem phenomena.

The difference in the body chamber/phragmocone volume ratio for phragmocones is the most important factor in limiting the maximum shell diameter that allowed ammonoid shells to either float or sink by means of pressure compensation. Theoretically, elongation of the body chamber reduced phragmocone volume and increased soft-body weight, so that a reduction in shell weight by shell thinning would be needed to maintain neutral buoyancy (Saunders and Shapiro, 1986). We calculated the largest body chamber/phragmocone volume ratio as 8.4, regardless of whorl-section shape, in a hypothetical ammonoid where the shell volume is minimal (shell thickness = 0.0133, and septal-
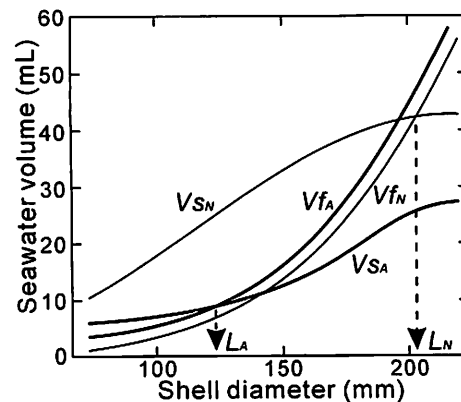

Figure 2. Estimate of limiting shell diameter in ammonoids that sank by pressure compensation of phragmocone. L_A, L_N—limiting diameters for hypothetical ammonoid with longest body chamber and *Nautilus pompilius*, respectively. Limiting diameters of most ammonoids approximate that of *N. pompilius*. Vf_A and Vf_N—limit of seawater volume in phragmocone that still allows flotation for hypothetical ammonoid with longest body chamber and *N. pompilius*, respectively. Vf_A is slightly higher than Vf_N due to volume increase of body chamber: Vf_A = (difference of density between soft body and seawater) × (volume of body chamber). Vs_A and Vs_N—seawater volume needed for pressure compensation by ammonoid with longest body chamber and *N. pompilius*, respectively. Vs_A is smaller than Vs_N due to volume decrease of phragmocone: Vs_A = (volume of phragmocone) × [1 − (total gas pressure of phragmocone)].

siphuncle factor = 1.052; see Saunders and Shapiro, 1986), assuming that total gas pressure in the phragmocone and the density of the shell and soft body were the same for ammonoids and *N. pompilius*. This value is similar to that of an actual ammonite (8.5 in *Liparoceras* aff. *cheltiense*) with the largest known body chamber/phragmocone volume ratio (Trueman, 1941). We determined the limiting shell diameter as ~120 mm for this hypothetical ammonoid, by calculating the maximum seawater volume in phragmocone-supported flotation (Vf_A) and the maximum volume of seawater taken in due to pressure compensation (Vs_A) (Fig. 2). The body chamber/phragmocone volume ratio for the majority of Jurassic and Cretaceous ammonoids analyzed by Trueman (1941) approximates those of *N. pompilius*. This fact strongly suggests that the limiting shell diameter that negated flotation by pressure compensation for most ammonoids was similar to that for *N. pompilius* (i.e., ~200 mm).

To some extent, ammonoid shells may have behaved differently from *N. pompilius* because of their wide variety in shell geometry. Ammonoids generally have a body chamber longer than *N. pompilius*, and the shell aperture of many is considered to have been ori-

ented obliquely upward during life (e.g., Trueman, 1941; Raup, 1967; Saunders and Shapiro, 1986). This suggests that the soft body of an ammonoid was more stable and remained longer within the body chamber than in *N. pompilius*, and therefore that ammonoids had a better chance of being preserved in situ. This view is apparently supported by the fact that the in situ preservation of jaw apparatuses in body chambers has been documented more often in ammonoids than in nautiloids (Saunders et al., 1978).

In ammonoids, the speed of waterlogging by seawater flooding into the phragmocone may have been controlled by the radius, thickness, and length of the siphuncular tube. The first two factors can be accounted for by the siphuncle strength index (100 $\times$ wall thickness/inner radius) defined by Westermann (1971). He showed that the Jurassic and Cretaceous ammonoids he examined have indices similar to, or smaller than, modern nautiluses. In contrast, the indices of the suborder Phylloceratina and Lytoceratina are ~1.5 times larger than those of modern nautiluses. The siphuncle length depends upon its position within the phragmocone and the coiling pattern of the shell. The more ventrally positioned the siphuncle, and/or the smaller the rate of whorl expansion, the longer the length of the siphuncle. Our examinations suggest that the ammonoid siphuncle is ~1.5 times and ~3.0 times as long as *N. pompilius* when the tube is positioned at the most ventral side in tightly and gently coiled shells, respectively. These facts suggest that the rate of waterlogging in ammonoids was either the same as, or faster than *N. pompilius*. An exception to this is the Paleozoic suborder Clymeniina, in which the siphuncle is positioned dorsally. Furthermore, for ammonoids with long septal necks (see Tanabe et al., 1993), which involved shortening of the siphuncle, the waterlogging rate might have been slower.

Although postmortem drift has been frequently invoked in taphonomic studies of ammonoids, unequivocal evidence for this drift is very scarce. Kase et al. (1994, 1998) observed that the only examples of long-distance drift in ammonoids were inferred from infestations of pelagic limpets. Such ammonoids are mostly >200 mm in diameter, consistent with our interpretation. In conclusion, we suggest that (1) only large ammonoid shells (>~200 mm in diameter) had the potential to drift postmortem over long distances, and (2) most shells (especially small ones) rapidly

sank near their habitats, even if they once floated.

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