**Palaeontologia Electronica**
http://palaeo-electronica.org

# A REVIEW OF THE POST-MORTEM DISPERSAL OF CEPHALOPOD SHELLS

Richard A. Reyment

## ABSTRACT

Among invertebrates, the distribution of chambered cephalopods constitutes a special case owing to their potential for post-mortem dispersal. The earlier prevailing opinion of many, but far from all specialists, that shells accumulated at, or close to, their areas of living distribution, in the same manner as gastropods, has been supplanted by a wide acceptance, that nekroplanktonic dispersal is the rule rather than the exception. The basis for this swing is mainly ascribable to increased knowledge of the post-mortem dispersal of the shells of extant nautiloids and improved extrapolation of these results to palaeobiogeographical interpretations of ammonite distribution. A new element explored here is that of the significance of encrusters, such as oysters, as a tool for studying the taphonomy of nekroplanktonically spread ammonites.

Richard A. Reyment. Palaeozoological Section, Swedish Museum of Natural History, Box 50007, Stockholm, Sweden. Richard.Reyment@nrm.se

**KEY WORDS:** nautiloids; ammonites; post-mortem dispersal; Indian Ocean; Pacific Ocean; encrusters

## INTRODUCTION

My interest in taking up the subject of the post-mortem dispersal of cephalopod shells in 1957 came from a review and critique by Jaworski (1940) in *Neues Jahrbuch* of an article by G. Scott (1940) in which a palaeoenvironmental model for Texan Cretaceous ammonites was put forward. Jaworski (1940) pointed out the illogicality of a 'palaeohistory' for chambered shells as though they were gastropods. Scott did cite, however, a few records of the nekroplanktonic transport of empty nautilus shells in his discussion. In the analysis of the post-mortem dispersal of cephalopod shells we are not concerned with organisms as such, but with the passive distribution of "objects" by oceanic currents, and hence under conditions defined in a different medium from that occupied by the living animal. The opinions of workers in the field have centred around attempts at relating shell-forms to specific activities extending as far as to drawing conclusions about cephalopod shells as environmental indicators, as opposed to factors relating to the post-mortem dispersal of the shells. From the standpoint of the palaeontologist, the fundamental issue concerns what happened to the empty shell after the death and decay of the animal.

Since the appearance of my original contributions from 1958 to 1986, I have followed develop-

PE Article Number: 11.3.12A

Submission: 29 December 2007. Acceptance: 29 April 2008

Reyment, Richard A. 2008. A Review of the Post-mortem Dispersal of Cephalopod Shells. *Palaeontologia Electronica* Vol. 11, Issue 3; 12A:13p; http://palaeo-electronica.org/2008_3/148/index.html

ments in the field of the distribution of fossil cephalopod shells. An observation arising out of this research is that in some cases, 'the wheel keeps getting rediscovered', as it were. There is a source of uncertainty, namely, the confusion occasioned by failing to accept that what the ammonites and nautiloids did in life has little or nothing to do with what happened to them after death. After all, the history of pieces of wood that float up onto beaches has little to do with where the trees from whence they derive once lived.

The following assumptions provide a convenient basis for discussion:

1. Various dead chambered shells would have been amenable to palaeoflumenological dispersion, to use the term introduced by Kobayashi (1954).
2. An unspecified number of shells with specific morphological characteristics, with a benthic mode of life, may have remained near, or close to, where they died.
3. Some shell-types lent themselves to a short period of nekroplanktonic dispersal, before sinking. Others could remain afloat for long periods.

The cases reviewed here may be conveniently considered in the following order. Firstly, the information available for the paradigm, the pearly *Nautilus*, secondly, extrapolation to the ammonites and, thirdly, the case represented by some Palaeozoic nautiloids (orthocones, cyrtocones, etc.).

## THE LIVING PARADIGM: THE PEARLY NAUTILUS

The sole living representatives of the coiled, chambered cephalopod shell, apart from *Spirula*, are species of *Nautilus*. With the pearly nautilus as a standard of reference, the temptation to extrapolate thoughts and observations to the extinct group of ammonites is understandable. In the 50 years that have elapsed since the appearance of my monograph on the subject of post-mortem distribution of cephalopod shells (Reyment 1958), I have seen opinions wax and wane until it now seems clear that experts in the field have embraced the view that the general rule must be that dispersal of shells by marine currents is a major factor, notwithstanding that *in situ* deposition can occur and has no doubt taken place (the "gastropod-mode"). Results reported in Wani (2004, 2007) and Wani et al. (2005) have brought to light a possible explanation for the segregation of mature shells from juvenile shells, sometimes observed Recently defunct juvenile shells may become more readily waterlogged than adults and hence could be buried in sediment near to where they lived. This forms the basis of a model, which might be applicable to some ammonite occurrences and would explain the atypical age-pyramid from time to time encountered in shell accumulations. However, the model for age-differentiation reflected in the occurrence of ammonite shells contains an element of unreality in that it presupposes, tacitly, that juvenile mortality in shelled cephalopods, past and present, is exceptionally high and that all growth phases share an equal opportunity of being preserved post-mortem. This hypothesis has yet to be objectively tested. There is also the differentiation in morphology usually seen in micromorphic and macromorphic ammonite shells. In species of the Cretaceous genus *Knemiceras*, to cite an example, dimorphism is pronounced yet size-related differentiation with respect to preservation in occurrences is not observed in any of the large collections known to me. However, the late Professor Tove Birkelund once showed me material of heteromorphic Cretaceous ammonites from Greenland, which I now believe could have represented macromorphs and micromorphs in two size groups.

Kobayashi seems to have been the first to formalize the concept of the post-mortem distribution of cephalopod shells when he introduced the term "palaeoflumenology" into the scientific literature (Kobayashi 1954). Kobayashi was concerned with explaining the occurrence of *Aturia* in the Miocene of Japan. Part of his reasoning was based on an analogy with the post-mortem distribution of living *Nautilus*, shells of which are carried by the Kuroshio current from the Philippines. Kobayashi (op. cit.) also reported the occurrence of drifted *Nautilus* shells at Misaki near Tokyo (NB. one of the marine biological stations of Tokyo University is located at Misaki, Tokyo Bay) and stressed the fact that these occurrences are several thousand kilometers from their natural habitat. Other exotic occurrences noted by him are Lao Chao Island, New Zealand beaches, New South Wales, the Nicobar Islands and Sunday Islands. Wani (2004, 2007), who in commenting on the evidence for the nekroplanktonic dispersal of nautiloid shells (and occasional living individuals) as far as Japan, thought that the distance involved was too great to be reasonable and that some nearer natural habitat would be more likely. He appears to be unaware of the evidence for wide dispersal of *Nautilus* spp. extending to the western Indian Ocean, registered in the pertinent literature, and summarized and annotated by

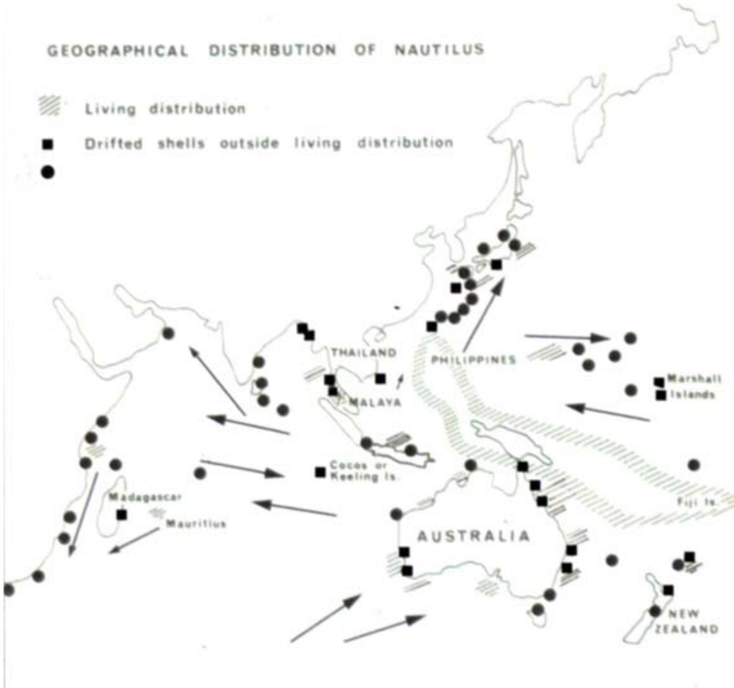

**Figure. 1.** Updating of the sketch map published in Reyment (1973) illustrating the geographical distribution of *Nautilus s. l.* in the Pacific and Indian Oceans. This figure includes information from the maps of House (1987, figures 1, 3) and more recently acquired data. The arrows denote major oceanic currents of presumed significance for the nekroplanktonic and living distributions of *Nautilus.* The black dots denote reports of nekroplanktonically dispersed shells since the original sketch-map of Reyment (1973) was published. The earlier reports are represented by black squares.

House (1987). A similar remark can be applied to the opinion expressed in Machalski et al. (2007) with respect to the dispersal of scaphitids, at least as far as can be concluded from the brief discussion in their text. Toriyama et al. (1965) summarized information on drifted shells stranded on the islands of Ko Phe Tra and Ko Tarutao on the western coast of Thailand. The finds at Ko Tarutao occur high up on the beach, together with driftwood, *Sepia* shells and in the fringing zone delineated by shrubs and grass. The relatively large proportion of partially broken shells accords well with what occurs along the western coast of Malaya (Reyment 1973, p. 36) and with what Teichert (1970) recorded for islands off the Burmese coast in the Bay of Bengal. While on this subject, the interpretation of shell breakage caused by collisions between drifters, as promoted by Wani (2004), although possible in rare cases, should be kept within reasonable perspective. A common source of shell damage is due to wave action smashing shells against reefs and to swash abrasion in a pebbly shore-zone.

While working at Kyushu University, Fukuoka, in 1973, I learned that some primary schools support a project for recording occurrences of nautilus drifts, not only on the southern coastline of Kyushu but also further north on the eastern seaboard of Honshu. This information, and Kobayashi's (1954) results, paved the way for an analysis of the occurrence of nautiloids in the Paleocene of Nigeria. It was concluded that the few shells found so far had been nekroplanktonically transported by the Benguela Current from the Cabinda region (Reyment 1967). Chirat (2000, p. 72) arrived at an analogous explanation for the post-mortem distribution of Cenozoic *Aturia* in the Neogene deposits of the Aquitaine Basin (France).

Reyment (1958, p. 112) quoted Mr. D. Hall of the Singapore Fisheries who supplied information on finds of nautilus shells found during trawling. In 300 trawls in the South China Sea by the R. V. *Manihine* no live individuals were brought up, and only three damaged shells were found in the nets. Teichert (1970) reported on the nekroplanktonic dispersal of shells of *N. pompilius* in the Bay of Bengal; he estimated the distance of post-mortem transport as being around 3000 km from the nearest known habitat of the species. It is now known that the pearly nautilus occurs in waters off the western coast of Thailand and Malaya, thus reducing the estimate of 3000 km for the nekroplanktonic dispersal of shells in the Bay of Bengal, given by Teichert, to around 800 km. In the same note he brought together some little-known published information on drifted shells, including the occurrence of a shell found floating 200 km SW of Sri Lanka and one collected from north of Madagascar. Stenzel (1964, p. K88) referred to drifted shells found on the eastern coastline of Madagascar (see also Dautzenberg 1923). References to living individuals and drifted shells recorded in the western Indian Ocean are documented in House (1987, figure 1), and there is a reference in Lehmann (1964, p. 192).

My sketch-map for the distribution of *Nautilus* spp., living and transported (Reyment 1973, p. 38), is based on information in Stenzel (1964), Teichert (1970) and, with respect to the western reaches of the Indian Ocean, a letter dated December 5, 1967 received from Dr. Anna Bidder (Cambridge). Dr. Bidder informed me that she “now had evidence of living *Nautilus* from Mauritius and Zanzibar.” The biogeographical status of these occurrences is still poorly understood; it is, however, clear that they simplify the interpretation of post-mortem distribution of shells in the western Indian Ocean. The sketch-map (Reyment 1973) shows the occurrence of living *Nautilus* off South Australia. That observation is based on the report of the capture of a single living specimen off Foul Bay in 1911 (Iredale 1944). Stenzel (1964, p. K88) referred to two stranded individuals found of the coast of southern Australia. Moreover, living *Nautilus* occur off Albany in the western extremity of the Great Australian Bight. In the normal case, *Nautilus* is believed to be restricted to warm tropical waters, but the southern Australian data indicate that even cooler waters can be tolerated. An updated version of the sketch-map from 1973 referred to above (Figure 1), based on new observations, and augmented with data from House (1987, figures 1 and 3), gives the impression that outside the main area of distribution of species of *Nautilus* in the western Pacific Ocean, there is a large area in which living individuals and drifted shells occur much more sparsely. Examination of Figure 1 possibly provides a clue to this seeming anomaly, notably, that the regions of greater population density lie in coral seas. The lesser densities are located in the outskirts of the geographical range of the genus where analogous underwater structures to coral reefs are scarce or lacking. This is the case for Japanese waters and to a fair degree, the eastern zones of the western Indian Ocean and the Great Australian Bight. House (1987, figure. 3) related the pattern of drifted shells, and living distributions, to the ocean currents of the Indian and Pacific Oceans and could recognize the existence of a clear relationship between the shell-drift pattern and known main oceanic currents. Shells of *Nautilus* are reported to be well known to inhabitants of the eastern African coastline; evidence is provided by the issue of a postage stamp by Kenya depicting a stranded *Nautilus* shell (pictured by House 1987, p. 56, figure 2). References on experiments for flotation times of chambered cephalopod shells are noted by Saunders and Spinosa (1979) and Hewitt (2006). Ekman (1953) summarized the role of large-scale oceanic currents for the dispersal of various organisms.

Sinclair et al. (2007) reviewed aspects of the population dynamics of *Nautilus* spp. in a molecular biological analysis using the cytochrome oxidase subunit I (Cox I). In their explanation of the biogeographical elements found in their study, they thought that it might be possible, but unlikely, for animals to survive for months in cooler water. The fact that *N. pompilius* descends readily to depths of several hundred metres for foraging can be taken to indicate that it is a eurythermal animal. The solution to this enigma, as noted above, is contained in House’s study, which says that at least some species of *Nautilus* are able to survive under presumably less than optimal conditions, such as pertain, for example, in the Great Australian Bight.

In a fisheries paper describing the exploitation of living molluscs of the Philippines, Talavara and Faustino (1931) considered commercial aspects of the biology of *Nautilus pompilius*. They reported the species to be abundant off the southern coast of Negros, Tanon Strait, Bantayan, Gebu Palaman, Cuyo, Basilan, Leyte and Mindoro in a coral-bottom environment. Although animals were caught in traps set as deep as 400-600 m, most catches were made at depths around 60 m. Empty shells are commonly picked up along beaches or in shallows.

### Moribund State

The question arises as to the final phase of life in a dying nautilus. Rather than just giving up the ghost in a few seconds, as might be surmised from some interpretations, it is far more likely that the animals go through a phase of death throes. It is known that moribund nautilus individuals (Karnovsky scale 10<20 units) have difficulty mustering the energy for maintaining zero, respectively negative buoyancy. Cameral liquid is therefore dissipated during the death-phase. None of the shells I dissected during my stay in the western Pacific Ocean in 1968 were found to contain significant amounts of cameral liquid in any of the chambers. This evidence accords with the observations recorded by Bidder (1962) and Denton and Gilpin-Brown (1967). It seems evident, therefore, that cameral liquid is quickly lost in the shells of dying individuals in consequence of which perishing animals embark automatically on a last journey to the surface.

## EXTRAPOLATION TO THE POST-MORTEM DISTRIBUTION OF AMMONITES

Reyment (1958) presented a review of the opinions of earlier workers on the taphonomy of fossil cephalopods. A brief resumé of these notes is given below, granted that my original monograph is not widely available. Walther (1897, p. 258) realized the importance of the problem under review as did, later, Lehmann (1964, p. 14). Walther referred to, in his opinion, the inexplicable lack of ammonite soft parts allowing that impressions of body parts are known of belemnites and other cephalopods and was led to assume that empty ammonite shells could float for a period of time (Walther 1897, p. 261, 262). Rothpletz (1909) monographed the fossils of the Solnhofen beds. In this work he observed that aptychi are present in the body chambers of some of the ammonites and concluded that such occurrences represent early burial of individuals in a tidal flat environment. Further discussion of Rothpletz' observations can be found in Reyment (1958, pp. 103-104). Emulating Rothpletz' research, Reyment (1970b) collected field information on vertically imbedded ammonite shells of ceratitids as well as other forms, *Choffatia*, for example, and ventral impressions in sediment (cf. Chamberlain and Weaver 1978). A specimen of *Nautilus macromphalus* from New Caledonia received in 1957 from Dr. F. McMichael of the Natural History Museum of New South Wales, and collected in 1882, was still poised upright in formalin in its container when it arrived in Stockholm (Reyment 1958, p. 134) .

Reyment (1973, 1980) constructed models of ammonites to examine their post-mortem spreading capabilities. Models of *Ceratites nodosus* and *Discoceratites* sp., based on material from the Triassic of Main-Franken, Germany, were found to float higher in salt water than shells of *Nautilus* spp. Highly evolute ammonites were modelled on *Morphoceras* (Middle Jurassic) and *Dactylioceras* (Lower Jurassic). The empty shells of such forms float horizontally oriented, like a floating pancake as it were. In life, the shell floats vertically and is noticeably static with a marked moment of inertia. By the courtesy of the Trustees of the Swedish Natural History Museum, Stockholm, the text of Reyment (1973) can be accessed at http://www.nrm.se/download/18.40476b02115a35bea038000321/Reyment_1973.pdf.Scott (1940) proposed a bathymetrical zonation based on the shape and ornament of Texan Cretaceous ammonites. His ideas were based on the assumption that nekroplanktonic dispersal of empty shells would have been an exceptionally rare event. Scott seems to have been largely unaware of observations on living nautiloids. Occasionally, Scott's Texan model shows up in general textbooks on palaeontology by "non-experts" but for the most part it has been consigned to oblivion. Arkell (1949) was uncharacteristically ambivalent with respect to the post-mortem dispersal of ammonite shells. He thought (1949, p. 408) that on death, shells sank to, or remained on, the bottom and stayed there. Further on in the same publication, however, he (Arkell 1949, p. 413) contemplated the wide dispersal of many species. Later, Arkell (1952, p. 15) changed stance entirely and concluded that drifted shells of Jurassic species ended up as part of stranded material along the shoreline, mixed with plant and vertebrate remains. The Jurassic locality at Brora (Scotland), interpreted for me in 1968 by Professor Michael House, is particularly informative; here kosmoceratid ammonites occur abundantly together with coalified wood (Reyment 1970b). Haas (1949, p.7) is a further useful reference for examining the extrapolation of observations on living *Nautilus* to ammonites. He noted that relatively compressed acanthoceratid shells occurred together with fossil wood, here and there charred, in the mid-Cretaceous near Greybull, Wyoming. This type of association mirrors what is found in the Pacific Ocean in the cast up flotsam on the shorelines of atolls. Similar occurrences can be observed in the Jurassic of southern Sweden (Skåne), as for example, at Katslösa.

The experimental studies reported in Reyment (1958) showed that the single most important factor among all interacting variables for deciding the post-mortem buoyancy capabilities of a cephalopod shell is the length of the body-chamber. The shape of the shell comes next in importance. A graphical procedure for appraising the buoyancy for ammonite and nautiloid shells was introduced by Reyment (1973, figure 32) using a multivariate Q-mode graphical procedure known as Principal Coordinates (Gower 1966). This figure was constructed using data on 42 species of coiled nautiloids and ammonites of a variety of shapes. This chart supplies a means of estimating, approximately, the likelihood of a coiled shell possessing a good nekroplanktonic dispersal capability. The statistical distances between "points" yield information on degrees of morphological similarity.

## ORTHOCONIC NAUTILOID SHELLS

Among earlier workers, Lindström (1890, p. 4) recorded the remarkable accumulations of lituitid and ascoceratid shells in Gotlandian sediments, which he interpreted as having been built up by shells stranding in near-shore shallows. In his discussion he related the occurrences to the drifting of the shells of modern *Spirula.* Kriz and Bogolepova (1995) recorded the parallel orientation of Silurian

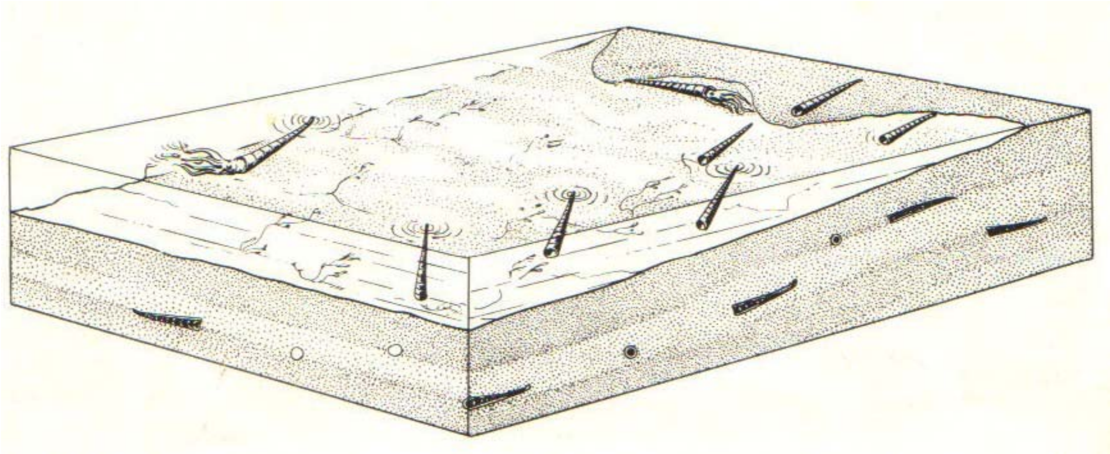

**Figure 2.** Artist's impression of the stranding environment at Såtatorp, Kinnekulle, Västergötland, Sweden during the Ordovician. Artist Mr. Eric Ståhl.

orthoconic shells due to current action. Laufeld (1974) described the occurrence of orthocones displaying preferred orientation in the uppermost Hemse Beds (Silurian of Gotland), which he could relate to an assumed current direction. Additionally, Laufeld (1974, p. 159) deduced that the calcareous deposits in some of the chambers of the nautiloids is not a primary feature but one deriving from the precipitation of calcium carbonate resulting from the chemical interaction with decaying soft tissue during early diagenesis. (N. B. the post-mortem fate of nautiloids with massive calcareous deposits is not considered in this review.) Laufeld's conclusions with respect to the post-mortem stranding of shells were inferred by applying a procedure based on circular statistics and introduced into palaeontology by Reyment (1971). A work in the same vein is that of Gnoli et al. (1979) concerning the post-mortem distribution and preservation of Silurian orthoceratites from Sardinia. Here, also, the methods of circular statistics as employed by Reyment (1971) were used.

Reyment (1968) analysed occurrences of *Rhynchorthoceras* in the Ordovician limestones at Såtatorp. Västergötland, Sweden. Preferred orientations of shells were studied by the above-mentioned methods of circular statistics with emphasis on the location of the siphuncle the siphuncular diameter of these shells is about one sixth of the total diameter of the shell. The statistical tests showed that within narrow limits of variation, the nautiloids at Såtatorp are oriented with the siphuncle roughly in the 270 degrees position, and that this orientation is not random (Reyment 1968, figure 2). It was concluded that the shells drifted into unconsolidated lime-mud in a direction at right angles to the shoreline (Figure 2) where they became fixed, largely undisturbed by swash-action (Reyment 1968, 1971).

Preferred orientation of orthoconic shells is not a general rule. Reyment (1970a) studied a superficially similar occurrence to that of Laufeld (1974) in the Ordovician of the Brunflo area in Jämtland, Sweden. That work disclosed that the orthoconic shells were randomly oriented both with respect to the length-axis and, in some cases, to the diametrical axis. It was concluded that current action had not played a decisive role with respect to orientation during the preservation of those orthocones. In paleoenvironmental terms, the random spread of the orientation of the siphuncle is such that it would seem that the shells had been rolled by swash on a relatively unyielding substrate such as algal matting.

Reyment (1973) demonstrated by means of models, that the free-floating (nekroplanktonic) orientation of orthocones and cyrtocones was vertical due to the deadweight of the body chamber. It was concluded by extrapolation, that the orientation of living orthocones and similar uncoiled shell-types, would have been vertical and that the "torpedo-model" is most likely a fanciful construction. A vertically oriented Ordovician cyrtocone from the Såtatorp locality is depicted in Figure 3. This occurrence might be an example of the vertical orientation model deduced by Chamberlain and Weaver (1978) for the final resting phase of cephalopod shells. A note of the vertical floating orientation of post-mortem floating turrilitid gastropods by Krejci-Graf (1932) is an instructive record here. From the aspect of feeding economy, a vertical orientation of the orthoceratid shell and cyrtocones in

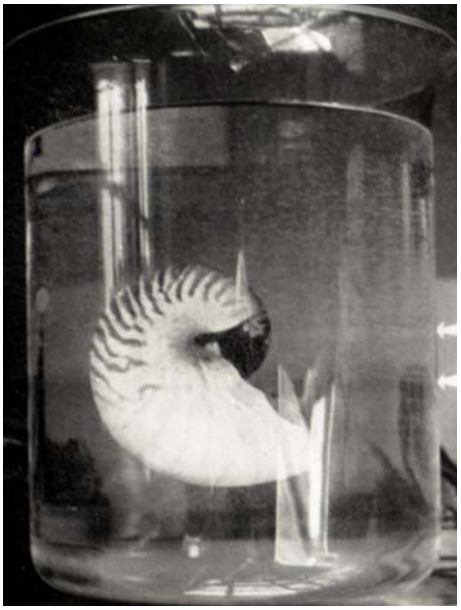

**Figure 3.** Detail of a laboratory experiment showing an almost waterlogged shell of *Nautilus pompilius* floating on the interface between freshwater (above) and water of normal marine salinity. The white arrows to the right mark the narrow zone of mixing between saline water and fresh water.

life is the only reasonable foraging model (browsing) available from the vital viewpoint of energy conservation (Reyment 1988). By way of interest, it is worth mentioning that refloated "mummified" echinoid tests can, under certain conditions, be nekroplanktonically transported (Reyment 1986).

## THE ROLE OF DEEP-WATER OCEANIC CURRENTS

Reyment (1958, pp. 158-160) investigated experimentally the effect of temperature and salinity stratification on the buoyancy of shells. Briefly summarized it could be shown that even a difference of 2-3°C was sufficient to either bring an almost waterlogged shell to sinking condition or, conversely, raise a partially waterlogged chambered shell from the bottom. Thermal stratification in modern oceans is well known (Münster-Strøm 1936) in which a treatise on the subject of salinity reaction currents was also treated.

The potential for submarine dispersal of shells by oceanic currents is probably great. In one experiment (Reyment 1973), it was found that a shell poised upright on the floor of the experimental tank responded quickly to even slight currents, being lifted from the bottom and sent skimming. Experiments on partially waterlogged shells by Wani and Ikeda (2006, p. 291) confirm Reyment's (1973) findings obtained using the flumes in the Department of Physical Geography at Uppsala University. Photographs of experimental results are given in www.nrm.se/download/18.40476b02115a35bea038000321/Reyment_1973.pdf.

**Figure 4.** View of a cyrtoconic Ordovician nautiloid preserved in an upright position. The quarry in the Ordovician at Såtatorp, Kinnekulle, Västergötland, Sweden.

Seilacher (1963, p. 599) deduced that something of the kind could have happened with fossilized ammonite material he studied but he invoked an unlikely mechanism of "bowling" i.e., shells being bowled along by currents as hoops in the manner of a popular children's game. The experiments accounted for in Reyment (1973) also showed that the more evolute shell of *N. macromphalus*, when propelled by a current over a bottom of unconsolidated sand, tends to fasten owing to the braking effect of sediment scooped into the body chamber. It requires a strong current to cause the shell to move all. The ammonite models of Reyment (1980) of the types *Paravascoceras*, *Pseudaspidoceras, Dactylioceras,* when poised on the bottom have the aperture raised further upward than the above-mentioned species of *Nautilus*, implying that a dragging motion over bottom sediment would have been less likely to be hindered than in the case of *N. pompilius.*

Related physically and hydrostatically to thermal stratification there is salinity stratification and reaction currents (Münster-Strøm 1936). Experiments showed that a waterlogged shell placed in saline water of two densities, less saline above and normal saline below, sank until it encountered the denser layer where it floated stably on the salinity interface (Reyment 1958). A detail of an experiment on buoyancy at a saline interface is shown in Figure 4. Post-mortem floating of chambered shells along a salinity gradient has yet to be explored in Nature. The salinity reaction current is a possible mechanism whereby sunken shells can be transported far inland into a bay owing to the outflow of freshwater. A classical site is the marine shell-mounds at Uddevalla in Bohuslän, west Sweden, where marine life was moved far inland by reaction currents, coming to rest beneath freshwater (Hessland 1943). The combined factors of thermal and salinity stratification coupled with the deflecting effects of sea currents takes the credibility of the "crash-dive" model of submarine maneuvering for nautiloids out of consideration.

## CLIMATIC CATASTROPHES

Periodically, heavy rainfall in the tidal flat environment of the North Sea can bring about the mass mortality of the calamar. This is not invariably the case, however, inasmuch as these cephalopods are migratory, and it is only during their periods in the tidal zone of the North Sea that they run the risk of succumbing to a salinity catastrophe. In June 1969, there was such an episode in the Danish tidal flats at Esbjerg, the effects of which I witnessed in the company of a party of my research students. Thousands of dead calamars were observed stranded along the upper tidal zone after prolonged heavy rain had lowered the salinity level.

Can such an event be identified in fossil material? The answer is yes, at least in the case of broad epicontinental environments. For example, in the region just south of the Damergou of Niger Republic in deposits of the Saharan epicontinental sea of the early Turonian, great numbers of monospecific *Nigericeras* can be observed strewn over a flat, marly surface, presumably the victims of a sudden drop in salinity due to heavy rain (Schöbel 1975; Courville and Thierry 1993; Reyment 2003). The pictures of "stranded" orthocones in Gnoli (2003) bear a striking resemblance to the stranded individuals of *Loligo vulgaris* mentioned above.

## ACCURACY OF MODELS

The models used in my experiments accounted for in 1973 and 1980 were produced by sculpting a particular species in plastic material and then raising it to its appropriate specific weight by copper-plating (Reyment and Eckstrand 1957). Needless to say, the success of such an enterprise depends greatly on the skill and learning of the technician charged with the task. This work was undertaken by a professional sculptor, Mr. Eric Ståhl, and for the second part of the work, requiring special facility in working with plastics, by Mr. Bertil Annell. An idea of the accuracy of our modelling technique may be gained from Figure 5 where an original shell of *Nautilus pompilius* is shown together with a model. It will be seen that the floating capabilities of both are nigh on identical.

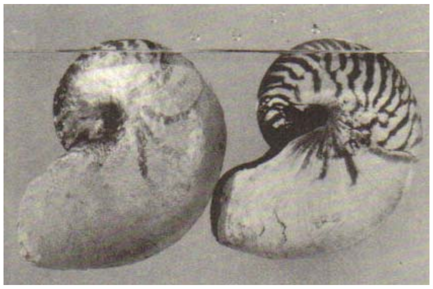

**Figure 5.** Comparison of a shell of *N. pompilius* floating beside a model of a similar specimen, constructed by Messrs Ståhl and Annell as described in the text. This experiment was carried out in order to test the accuracy of the modelling technique utilized in the experiments. Photo by Gustav Andersson.

The models were made from actual specimens as follows. The shells were dissected and the component parts for the models constructed by means of a commercial vacuum-moulding machine. This technique proceeds by quickly sucking a preheated sheet of plastic of suitable thickness around a mould. Vacuum-moulding is a widely used method for manufacturing toys.

## INTERPRETING ENCRUSTS ON SHELLS

John (1909) observed that oysters are often found cemented on ammonite shells. Encrusts can also attach to living nautilus shells. In 1972 Professor G. Westermann showed me a specimen of *N. pompilius* in which the shell had been broken back, thereby exposing an oyster encrusted on the venter of an inner whorl. Hence, the encrustation must have taken place in life and, moreover, in water shallow enough for *Ostrea* to thrive. Oysters begin life with a pelagic phase of two to three weeks in duration, after which they develop a foot (the pediveliger stage) and then hasten to seek a hard substrate. The oyster paradigm *Ostrea edulis* inhabits preferentially the subtidal zone, but has been reported to live at depths around 80 m. This natural habitat of this species in the North Sea is placed by Schäfer (1962, p. 567) in his Biofazies 7, to wit, 10-20 m.

In the majority of instances, nautiloid encrustations occur in several ways as was reported from the deep-sea expeditions under the leadership of Carl Chun (1910), who drew attention to the occurrence of drifting nautilus shells overgrown with encrusters of several kinds. Teichert (1970, p.

**Figure 6.** Two views of an encrusted specimen of *Knemiceras* (Lower Cretaceous (Albian) , Iran) showing oyster encrustations on the flank and venter. Photo by W. James Kennedy, Oxford.

1129) recorded two oyster encrustations inside the body chamber of a specimen collected in the Bay of Bengal. Palaeontological studies of encrusted cephalopod shells have been made by Meischner (1968), Merkt (1966), and Schindewolf (1934). *Placunopsis ostracina* is frequently found as an encrustation on shells of ceratitids. Geisler (1939) and Meischner (1968) showed that this encruster could settle on both living animals as well as drifted shells. Geisler (1939) obtained the evidence for the settling of *Placunopsis* larvae on living *Ceratites* by systematically breaking back shells as was done by Westermann, referred to above. (NB the taxonomic status of the encrusters of the Triassic, referred to *Placunopsis*, is uncertain.).

The monograph by Taylor and Wilson (2003) contains much information on encrusters. With respect to chambered cephalopods, they observe (Taylor and Wilson, 2003, p. 21) that shells of living *Nautilus* often support zoobiotic communities in which more than 90% of the shells are reported to be colonized in mainly the umbilical region by bryozoans, foraminifers, serpulids and barnacles. Drifted shells tend to be more heavily colonized and with the organisms more randomly distributed over the shell surface.

Several examples of encrusting by oysters on shells of species of the Albian genus *Knemiceras* from Iran and Lebanon have been recorded by W.J. Kennedy and myself. These are

1. One or the other of the flanks encrusted, with or without encrusters on the venter.
2. Venter only encrusted.
3. Both flanks fouled with or without encrusting oysters on the venter.

A significant feature of the material concerns the relatively high percentage of encrusted shells. Oysters are denizens of shallow water and it is therefore clear that the encrustation takes place on stranded, and stranding, empty shells, or on shells inhabiting shallow water. Case 1 represents oysters settling on dead shells lying near to the strandline and within the living range of oysters. Case 2 and Case 3 indicate fouling of floating ammonite shells by oysters. A specimen of *Knemiceras* from Iran bearing oysters on its venter and lateral flank is illustrated in Figure 6. A specimen of the early Turonian species *Wrightoceras wallsi*, from the Gombe area of Northern Nigeria, shown in Figure 7, bears numerous encrusting *Ostrea olisiponensis* from more than one infestation. The specimen appears to have ended up on its side in shallow water. Heavily fouled floating shells of the pearly nautilus have been recorded by Jokiel (1989) and also by Castillo and Guiñez (2000) with encrusts of coral, algae, oysters, barnacles, bryozoans and other organisms. Jokiel used his data to illustrate the geographical spread of organisms by rafting, that is, their being dispersed passively attached to floating objects. House (1987) cites an example for *N. scrobiculatus.* Westermann and Tsujita (1999, pp. 310-311) also made a clear statement of the roll of the nekroplanktonic factor in the dispersal of ammonites.

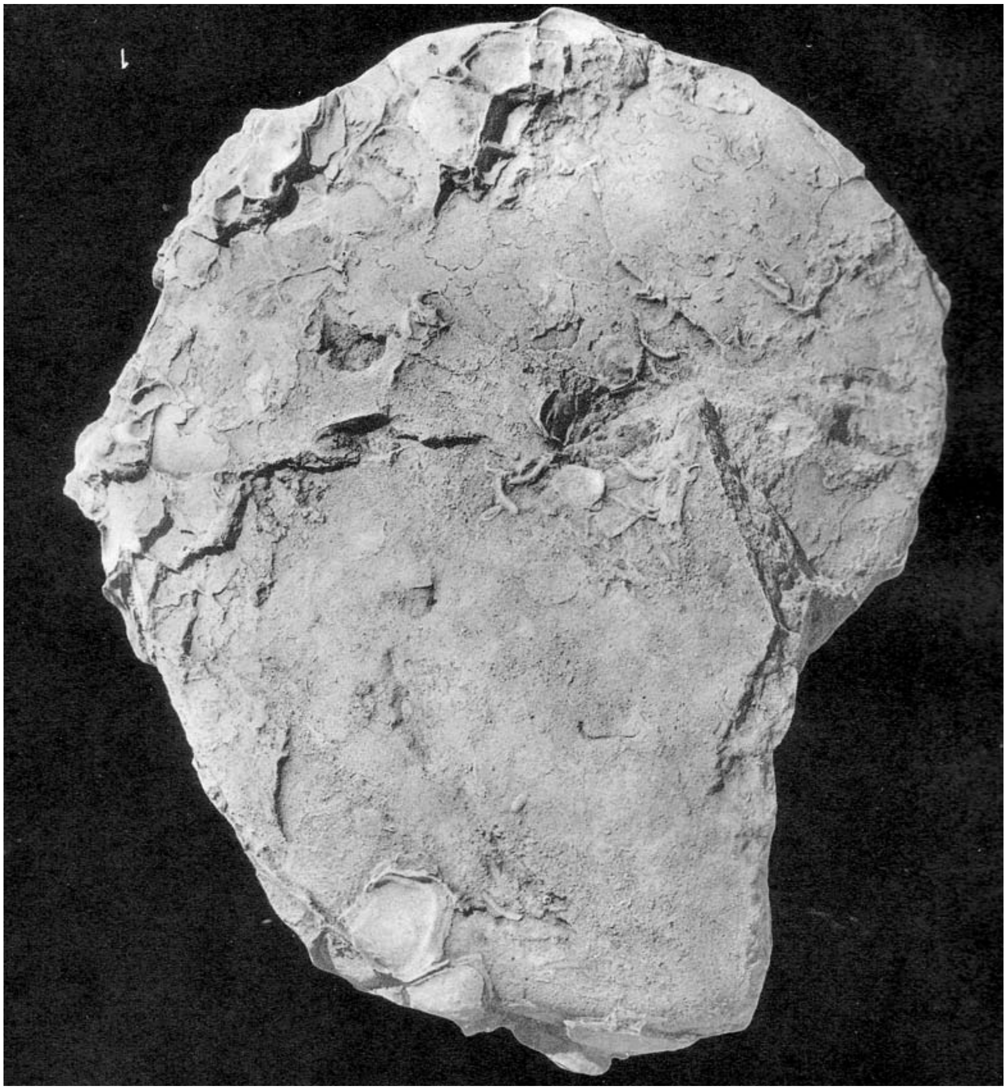

**Figure 7. L**ateral view of the early Turonian ammonite species *Wrightoceras wallsi* from the epicontinental sequence of one of the Saharan transgressions exposed at Gombe, NE Nigeria (diameter = 140 mm). The shell is heavily fouled by *Ostrea olisiponensis*.

## CONCLUDING REMARKS

"It is clear that adult shells of *Nautilus* may float for considerable periods after death" (House 1987, p.62). With this statement by one of the foremost cephalopod specialists of our time in hand, the reader will possibly wonder what I am hoping to gain by going over some of the same ground again. The reason is simple, namely, that despite the firmly documented status of our knowledge of the post-mortem fate of chambered shells, unsupported opinions to the contrary continue to appear presumably owing to unfamiliarity with the classical literature. House (1987), in his summarizing comments respecting maximum flotation times for shells of species of *Nautilus,* cites a record by Ishii made in 1981 of an example of a flotation period of 11 years for a tagged specimen. House attempted to explain the disjunct distributional pattern of *N. pompilius* by suggesting the possibility that shells from western Australia could be carried by currents to East Africa, alternatively, the continuation of the Borneo-Indonesian current might provide the means of transport of shells to eastern Africa.

The nekroplanktonic transport of shells in shallow epicontinental seas, such as the Saharan Cretaceous-Cenozoic episodes, is obviously seldom a question of first-order palaeobiogeographical significance, nor is the factor of depth-related distribution of the live animal in that environmental setting, owing to the shallowness of epicontinental transgressions. The range of environments in which ammonites were at home seems to have been greater than what pertains for living *Nautilus.*

## ACKNOWLEDGEMENTS

Professor N. MacLeod, Natural History Museum, London, provided invaluable help to the project by tracking down references. The technical staff of the Palaeontology Department, Swedish Natural History Museum, Stockholm, gave much appreciated technical assistance in various ways.

## REFERENCES

Arkell, W.J. 1949. Jurassic ammonites in 1949. *Science Progress*, 147: 401-407.

Arkell, W.J. 1951-1956. Monograph of the English Bathonian ammonites. *Palaeontological Society Monographs*, 1-169.

Bidder, A. 1962. Use of the tentacles, swimming and buoyancy control of the pearly nautilus. *Nature,* 196:451-454.

Castillo, J.C. and Guiñez, R. 2000. Disjoint geographical distribution of intertidal and nearshore benthic invertebrates in the Southern Hemisphere. *Revista Chilena de Historia Natural,* 73,4:1-23.

Chamberlain, J.A. and Weaver, J.S. 1978. Equation of motion for post-mortem sinking of cephalopod shells. *Mathematical Geology*, 10:673-689.

Chirat, R. 2000. The so-called “cosmopolitan” palaeogeographic distribution of Tertiary Nautilida of the genus *Aturia* Bronn 1838: the result of post-mortem transport by oceanic palaeocurrents. *Palaeogeogeography, Palaeoclimatology, Palaeoecology*, 157:59-77.

Chun, C. 1910. Die Cephalopoden. *Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer Valdivia 1898-1899*. Volumes, 18, 1 and 2, 552 pp. Fischer, Jena.

Courville, P. and Thierry, T. 1993. Nouvelles données biostratigraphiques sur les dépôts cénomano-turoniens du Nord-Est du fossé de la Bénoué (Nigéria). *Cretaceous Research*, 14: 385-396.

Dautzenberg, P. 1923. Liste préliminaire des mollusques marins de Madagascar et description de deux espèces nouvelles. *Journal de Conchyliologie*, 68:21-74.

Denton, E.J. and Gilpin-Brown, J.B. 1967. On the buoyancy of the pearly nautilus. *Journal of the Marine Biology Association U. K.*. 46, 723-759.

Ekman, S. 1953. *Zoogeography of the Sea*. Sidgwick and Jackson, London.

Geisler, R. 1939. Zur Stratigraphie des Hauptmuschelkalkes in der Umgebung von Wurzburg. *Jahrbuch des preußischen geologischen Landesanstalts*, 59:197-248.

Gnoli, M. 2003. Northern Gondwana Siluro-Devonian palaeogeography assessed by cephalopods. *Paleontologica Electronica*. Vol. 5, Issue 2, 2A: 19 pp. http://palaeo-electronica.org/2002_2/gondwana/issue2_02.htm

Gnoli, M., Parea, G.C., Russo, F., and Serpagli, E. 1979. Paleoecological remarks on the “Orthoceras Limestone” of southwestern Sardinia (Middle Upper Silurian). *Memorie della Società Geologica Italiana*, 20:405-423.

Gower, J.C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika,* 53:325-338.

Haas, O. 1949. Acanthoceratid ammonites from near Greybull, Wyoming, *Bulletin of the. American Museum of Natural History.* 93, 39 pp.

Hessland, I.R. 1943. Marine Schalenablagerungen Nord Bohusläns. *Bulletin of the geological Institutions, University of Uppsala,* 31, 348 pp.

Hewitt, R.A. 2006. Floatation experiments on cephalopod shells in seawater in England. *The Drifting Seed*, 12:9-12.

House, M. 1987. Geographic distribution of *Nautilus* shells, pp. 53-64. In Saunders, W.B. and Landman, N.H. (eds.). *Nautilus*, *the Biology and Paleobiology of a Living Fossil*. Plenum Press, New York.

Iredale, T. 1944. Australian pearly Nautilus. *Royal Zoological Society N. S. W; Australian Zoology*, 10:294-298.

Jaworski, E. 1940. Referat: *Neues Jahrbuch* Referate iii, 1000-1004.

John, P. 1909. *Über die Lebensweise und Organisation der Ammoniten*. Dissertation (Tübingen), Hofbuchdruckerei zu Gutenberg, Stuttgart.

Jokiel, P.L. 1989. Rafting of reef coral and other organisms at Kwajalein Atoll. *Marine Biology*, 101:483-493.

Kobayashi, T. 1954. A contribution towards Paleo-Flumenology, science of the oceanic currents of the past, with a description of a Miocene *Aturia* from central Japan. *Japanese Journal of Geology and Geography*, 25:35-56.

Krejci-Graf, K. 1932. Senkrechte Regelung von Schneckengehäusen. *Senckenbergiana*, 14: 295-299.

Kriz, J. and Bogolepova, O.K. 1995. *Cardiola signata* community (Bivalvia) in cephalopod limestones from Tajmyr (Gorstien, Silurian, Russia)., *Geobios*, 28:573-583.

Laufeld, S. 1974. Preferred orientation of orthoconic nautiloids in the Ludlovian Hemse Beds of Gotland. *Geologiska Föreningens i Stockholm Förhandlingar ,* 96:157-162.

Lehmann, U. 1964. *Paläontologisches Wörterbuch.* Ferdinand Enke Verlag, Stuttgart.

Lindström, G. 1890. Ascoceratidae and Lituitidae of the Upper Silurian formation of Gotland. *Kungliga. Svenska Vetenskapsakademiens Handlingar,* N. F.23 (13), 54 pp.

Machalski, M., Jagt, J.W.M., Kandman, N.H., and Matchurova, N. 2007. The highest records of North American scaphitid ammonites in the European Maastrichtian (Upper Cretaceous) and their stratigraphic implications. *Acta Geologica Polonica*, 57:169-185.

Meischner, D. 1968. Perniciöse Epökie von *Placunopsis* auf *Ceratites*. *Lethaia*, 1:156-174.

Merkt, J. 1966. Über Austern und Serpeln auf Ammonitengehäusen. *Neues Jahrbuch, Geologie, Paläontologie, Abhandlungen*, 125:467- 479.

Münster-Strøm, K. 1936. Land-locked waters. Hydrography and bottom deposits in badly ventilated Norwegian fjords with remarks upon sedimentation under anaerobic conditions. *Det Norske Videnskaps-Akademi*,Mat. Naturv. Klasse, 7, 85 pp, Oslo.

Reyment, R.A. 1958. Some factors in the distribution of fossil cephalopods. *Stockholm Contributions in Geology*, 1(6):97-184.

Reyment, R.A. 1967. A note on Paleocene nautiloids from Nigeria. *Colonial Geology and Mineral Resources*, 10:47-55.

Reyment, R.A. 1968. Orthoconic nautiloids as indicators of shoreline surface currents. *Journal of Sedimentary Petrology,* 38:1387-1389.

Reyment, R.A. 1970a. Quantitative paleoecology of some Ordovician orthoconic shells. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 7:41-49.

Reyment, R.A. 1970b. Vertically inbedded cephalopod shells. Some factors in the distribution of fossil cephalopods 2, *Palaeogeography, Palaeoclimatology, Palaeoecology*, 7:103-111.

Reyment, R.A. 1971. *Introduction to Quantitative Paleoecology*. Elsevier, Amsterdam.

Reyment, R.A. 1973. Factors in the distribution of fossil cephalopods. Part 3. Experiments with exact models of certain shell type. *Bulletin of the Geological Institutions of the University of Uppsala*, N. S. 4: 7-41. http://www.nrm.se/download/18.40476b02115a35bea038000321/Reyment_1973.pdf

Reyment, R.A. 1980. Floating orientations of cephalopod shell model. *Palaeontology*, 23:931-936.

Reyment, R.A. 1986. Nekroplanktonic dispersal of echinoid tests. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 52:347-349.

Reyment, R.A. 1988. A foraging model for shelled cephalopods, pp. 687-703. In Wiedmann, J. and Kullmann, J. (eds.). *Cephalopods - Present and Past*. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Reyment, R.A. 2003. Morphometric analysis of variability in the shell of some Nigerian (Turonian) ammonites. *Cretaceous Research*, 24:789-803.

Reyment, R.A. and Eckstrand, O.R. 1957. X-ray determinations of some cephalopod shells. *Stockholm Contributions in Geology,* 1:91-96.

Rothpletz, A. 1909. Über die Einbettung der Ammoniten in die Solnhofener Schichten. *Abhandlungen der mathematisch-physikalischen Klasse der königlichen bayrischen Akademie der Wissenschaften, München*, Band 24 (Denkschrift 81), Abt. 2:313-337.

Saunders, W. B. and Spinosa, C. 1979. *Nautilus* movement and distribution in Palau, Western Caroline Islands, *Science*, 204:1199-1201.

Schäfer, W. 1962. *Aktuo-Paläontologie nach Studien in der Nordsee*. Verlag Waldemar Kramer, Frankfurt am Main.

Schindewolf, O. 1934. Über Epöken auf Cephalopoden-Gehäuse, *Paläontologische Zeitschrift*, 21:42-69.

Schöbel, J. 1975. *Ammoniten der Familie Vascoceratidae aus dem unteren Unterturon des Damergou-Gebietes, République du Niger*, *Publications of the Palaeontological Institution of the University of Uppsala*, Special Volume 3, Uppsala, 136 pp.

Scott, G. 1940. Paleoecological factors controlling the distribution and mode of life of Cretaceous ammonites in the Texas area. *Journal of Paleontology*, 141:299-323.

Seilacher, A. 1963. Umlagerung und Rolltransport von Cephalopodengehäuse. *Neues Jahrbuch Geologie und Paläontologie, Monatshefte,* 11, 593-615.

Sinclair, W., Briskey, L., Aspden, W., and Pegg, G. 2007. Genetic diversity of isolated populations of *Nautilus pompilius* (Mollusca, Cephalopoda) in the Great Barrier Reef and Coral sea, *Reviews in Fish Biology and Fisheries*, 17:223-235.

Stenzel, H.B. 1964. Living *Nautilus*. *Treatise on Invertebrate Paleontology.* Part 4, Cephalopoda, Nautiloidea, 19 pp.

Talavara F, and Faustino, A. 1931. Industrial shells of the Philippines. *Philippines Journal of Science*, 3:321-350.

Taylor, P.D. and Wilson, M.A. 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth Science Reviews*, 62:1-103.

Teichert, C. 1970. Drifted *Nautilus* shells in the Bay of Bengal. *Journal of Paleontology*, 44:1129-1130.

Thiel, M. and Gutow, L. 2005. The ecology of rafting in the marine environment. *Oceanography and Marine Biology: an annual review*, 42:181-264.

Toriyama, R., Sato, T., Hamada, T., and Komalarjun, P. 1965. *Nautilus pompilius* drifts on the west coast of Thailand, *Japanese Journal of Geology and Geography,* 36:149-161.

Walther, J. 1897. Über die Lebensweise fossiler Meeresthiere. *Zeitschrift der deutschen geologischen Gesellschaft,* 49:269-273.

Wani, R. 2004. Experimental fragmentation patterns of modern *Nautilus* shells and the implications for fossil cephalopod taphonomy. *Lethaia*, 37:113-123.

Wani, R. 2007. How to recognize *in situ* fossil cephalopods: evidence from experiments with modern *Nautilus*. *Lethaia* ,40:305-311.

Wani, R. and Ikeda, H. 2006. Planispiral cephalopod shells as a sensitive indicator of modern and ancient bottom currents: new data from flow experiments with modern *Nautilus pompilius*. *Palaios*, 21:289-297.

Wani, R., Kase, T., Shigeta, Y., and Ocampo, R. de. 2005. New look at ammonoid taphonomy based on field experiments with modern chambered shells. *Geological Society of America*, 33: 849-852.

Westermann, G.E.G. and Tsujita, C.J. 1999. Life habits of ammonites, pp. 299-325. In Savazzi, E. (ed.), *The Invertebrate Skeleton*. J. Wiley and Sons.