



# Non-invasive approach to shed new light on the buoyancy business of chambered cephalopods (Mollusca)

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## Abstract

Here we present a new non-invasive approach for buoyancy calculation of recent and fossil chambered cephalopods using computer tomography scans. The procedure was developed on a recent *Nautilus* shell. Our new method shows high potential to shed new light on the lifestyle and buoyancy control of extinct cephalopods like the ammonoids. Due to the easy access of many morphological features of the shell of the examined specimen and the non-invasive technique it can be used to re-study holotype material. The enlarged set of available morphological features for species discrimination can also be used for future cladistic analyses.

## 1 Introduction

Chambered cephalopods (Mollusca) first appeared in the middle Cambrian with *Plectronoceras* as their oldest representative about 520 million years ago. One of their apomorphic characters, the phragmocone a chambered part of the shell functioning as a buoyancy apparatus, allows them to live in the free water column in contrast to the bottom crawling gastropods from which the cephalopods are derived (Bandel 1983, Haszprunar 1996, 2000). Nevertheless, it is still under discussion when cephalopods became a part of the free water column and how their lifestyle was.

To clarify whether chambered cephalopods, like the extinct ammonoid group, could swim or not several attempts were made (e.g. Moseley 1838, Trueman 1941) to calculate the buoyancy of some cephalopod shells including the volume of ammonite shells in order to reconstruct their mode of life.

Trueman (1941) already faced the difficulties of mathematical calculation of the volume of the “normal ammonite” shell including all its irregularities. In the case of extant *Nautilus* he simply determined the volume of the complete shell by the displaced amount of water. To determine the volume of each single chamber the shell was cut in median plane and each chamber was filled with water. Also the weight of the entire shell including the outer shell, septa, siphuncle and soft body were calculated by Trueman (1941) with the septa less than 10% and the siphuncle about 1-2% of the weight of the entire shell. The latest known complex calculations were accomplished by Kröger (2002) and Longridge et al. (2009).

Trueman's (1941) data were re-evaluated by Heptonstall (1970) using modern estimates for cephalopod tissue and shell densities. It turned out that ammonoids must have retained a higher amount of cameral liquid in their chambers to maintain nearly neutral buoyancy compared to *Nautilus*. The mechanisms of buoyancy control of extant chambered cephalopods (*Nautilus*, sepiids and *Spirula*) have been clarified by the publications of Denton et al. (1961, 1967), Denton & Gilpin-Brown (1961a, b, 1966, 1971). It becomes clear that the approximate neutral buoyancy in *Nautilus*, *Sepia* and *Spirula* was achieved by changing the ratio of gas and liquid in the phragmocone by osmotic pressure in the siphuncular cells. Further, Greenwald et al. (1982) localized an osmotic pump within the epithelial cells of the siphuncle of *Nautilus*.

## 2 Nautilus

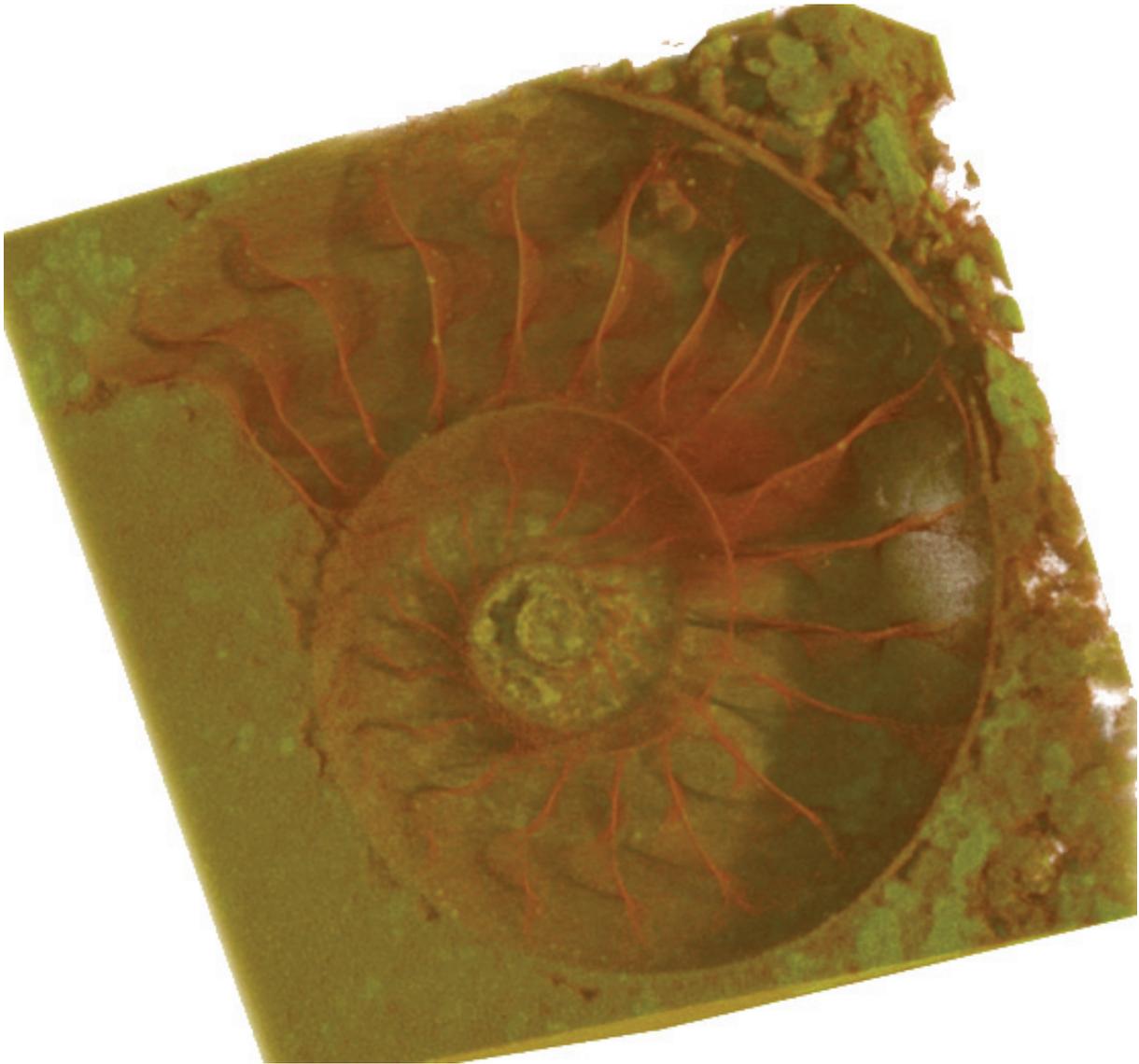
In this study we used a recent shell of *Nautilus pompilius* to establish our new method for calculating chamber volumes, shell volumes and mass of the entire shell. The adult *Nautilus* is largely dry in contrast to the shell of juveniles contain up to 32% of the total weight as chamber liquid. During ontogeny with increasing weight the volume of the chamber liquid decreases (Ward 1980). So that the juveniles maintain their buoyancy by coupling shell growth with the process of emptying liquid from the phragmocone (Collins et al. 1980), whereas in adults the small amount of chamber liquid is insignificant for buoyancy control. Noteworthy to say that juveniles of 70mm shell length recently have been reported to occur at 608m depth (Osprey reef part of the Great Barrier reef Queensland, NE-Australia) indicating that the hydrostatic apparatus is completely developed within the egg-capsule (Dunstan et al. 2011). However, throughout ontogeny *Nautilus* has slight negative buoyancy in seawater (Denton & Gilpin-Brown 1966, Ward & Martin 1978, Ward 1987). Although, the function of the buoyancy system in *Nautilus* and other chambered recent cephalopods is known, in ammonoids it is still under discussion.

## 2.1 Ammonoids

There are several attempts to explain the buoyancy mechanism in ammonoids by a) means of mathematical models (Moseley 1838, Trueman 1941, Heptonstall 1970, Reyment 1958, 1973, Mutvei & Reyment 1973) or b) by evidences from sublethal shell injuries (Kröger 2002) comparing datasets of *Nautilus* with mesozoic ammonoids or c) by explanation of an internal pressure-driven buoyancy regulation with the last septum functioning analogue to a fish-swim bladder (= “Cartesian diver model” of Seilacher & LaBarbera 1995). For further discussions see Jacobs (1996), Kröger (2002), and Hoffmann (2010).

Here we introduce the new non-invasive method for an accurate calculation of shell parameters such as chamber volume, chamber surface, ratio of chamber volume against surface, shell volume, shell weight, volume of the body chamber, ontogenetic changes of chamber volume and ratio of chamber volume / chamber surface as well as septal spacing and shell thickness) based on computer-tomography scans (ct-scans). Further, the potential of using 3D computer-models for the reconstruction of buoyancy mechanisms in chambered cephalopods is shown. In a first step this new approach was operated on the shell of extant *Nautilus*. Anyhow, the procedure developed has also high potential to be used for buoyancy calculation in ammonoids (Fig. 1). Detailed informations on the efficiency of the buoyancy apparatus of ammonoids will provide new insides to the paleobiology of this extinct cephalopod group. The potential of the new micro ct-technique to solve many of the unsolved questions of ammonoid paleobiology was recently demonstrated by Kruta et al. (2011) showing the first 3D ammonoid radula.

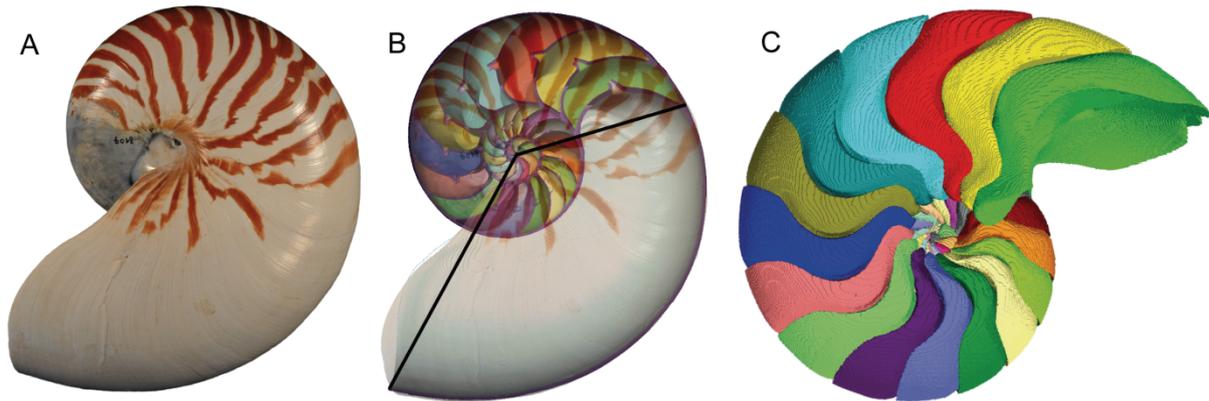
Retrospective, Lehmann (1932) was the first how tries to visualize the internal structures of ammonoids using stereo x-rays photographs. Later, the method becomes very popular for the analysis of the famous Bundenbach fossils (Stuermer 1970) but could never used for buoyancy calculations.



**Figure 1: A supposed *Eleganticeras* sp. (Lower Jurassic, Grimmen, N\_Germany) with about 1cm in diameter showing the rare hollow preservation. The specimen was scanned with a resolution of 6 micrometer voxelsize.**

### **3 Material and Methods**

One extant specimen of *Nautilus pompilius* from the Indian Ocean showing typical septal spacing of in total 34 chambers and a shell diameter of 158mm was investigated. The specimen is housed at the Ruhr Universität Bochum (Germany), Coll.-No.: 8107/2011. The last septa are slightly crowded including a lower volume than the preceeding chamber (Fig. 2), and a body chamber angel of  $136^\circ$  (Fig. 2B). For investigation the specimen was scanned by high-resolution computed tomography (v|tome|x s 240, GE Electronics Phoenix|x-ray) at the Steinmann-Institute (Bonn). The micro-CT images have a size of 1024 x 1024 pixels and isotropic voxels of 90 micrometer size. The 3D model was created using Amira® software.



**Figure 2: Extant shell of *Nautilus pompilius* of about 160mm in diameter, scanned with a resolution of 90 micrometer voxelsize. A: Photography. B: Combined figure showing internal structures. The number of chambers can be identified and the length of the body chamber (black lines) can be measured. C: Phragmocone showing 34 chambers each in a different colour to demonstrate that each chamber represents a single volume. Note the missing shell.**

### 3.1 Shell

Using the non invasive ct-scan technique makes it more easy to calculate various shell parameters without cutting the specimen studied. For all following calculations no Raup & Chamberlain (1967) equation or additional correction or extrapolation for different shell parameters is needed (compare Kröger, 2002). Thereby, for shelly material the error that occurs due to the use of equations with average values for volume approximation is deleted. Thus, ontogenetic changes in shell thickness will be recognized as well as different shell thicknesses at different whorl positions (ventral, lateral, umbilical). This would become more interesting when the method is transferred in order to analyze ammonoid shells in terms of ornamentation like ribs, nodes, constrictions and thinning outwards of the septal shelly material or apertural changes. For example: Kröger (2002) created a model for all ribs by a sinus curvature. An error may occur because ammonoid ribbing is never exactly radial, each rib can be different in height and width, ribs does not represent an ideal sinusoidal curve and is not perfectly regular.

### 3.2 Soft parts

Furthermore, difficulties for calculating the weight of soft parts remain. Our *Nautilus* specimen was stored for more than 30 years in the university collection and all soft parts disappeared a long time ago. These soft parts - like the animals body in the body chamber including the buccal mass (with chitinous radula and jaws), or the chamber connecting siphuncluar structure and the pellicle which cover the inner surface of each chamber working like a blotting paper during the emptying process of newly formed chambers - are usually not preserved in fossil specimens.

## 4 Buoyancy calculation

Taking that into account the possibility of direct measurement on the shell through ct-scan data the discussion of possible errors can be very short (compare with Kröger 2002 p. 67).

To calculate the volume of each chamber the total number of voxel per chamber were counted and multiplied with the voxel size. To achieve the total volume of all chambers their volumina were just added. To calculate the weight of the entire shell at first its volume was calculated by counting the total number of voxel. The calculated volume of the shell was than multiplied with the mean shell density of  $2.54 \text{ g/cm}^3$ .

To calculate the maximum buoyancy of the scanned *Nautilus pompilius* one must know the volume of displaced seawater which is identical with the total voxelnumber for shell material and chamber volume under the assumption that the whole body chamber is occupied by the soft body.

minus the sum of the mass of the shell wall, chamber walls, jaw apparatus and the soft body (including siphuncle, pellicle). For the soft parts we use a mean density of  $1.047 \text{ g/cm}^3$ .

Assuming that *Nautilus* live in near neutral buoyancy, the difference between calculated buoyancy and neutral buoyancy shows the mass of the liquid that occupied the chambers (fill fraction in the sense of Kröger 2002). For the buccal mass of the animals head region, includes the radula and the chitinous jaw apparatus, an average density of *Nautilus* jaw elements of  $1.655 \text{ g/ml}$  (Hewitt & Westermann 1993) is used here.

## 5 Morphology of shells

Besides the great advantage for buoyancy calculations of recent and fossil cephalopods it turned out that a lot of morphological data can be acquired with this method without destroying the specimens examined. That point might be very interesting for re-studying fossil cephalopod holotypes or extremely rare fossil cephalopod material for conch form analysis and morphological disparity. With this method exact description of external morphological features like ribs and nodes, shell wall thickness, whorl height, whorl width, whorl surface, whorl cross section shape and whorl expansion rate is possible (see Korn & Klug 2007). In addition several internal features e.g. position and diameter of the siphuncle, septal spacing, thickness of the septal wall are easily available. Further, ontogenetic changes of any observed feature can be described in an more precisely way.

In conclusion it helps to describe fossil cephalopod specimens more precisely and in a more objective way. The addition of some shell features used for specimen discrimination due to easy access should improve the knowledge of phylogenetic relationship among these groups based on cladistic analysis.

## 6 Problems

Problems for calculating exact buoyancy of recent and fossil cephalopod shells arise from the varying shell density reported by different authors for *N. pompilius* and *N. belauensis* ranging from  $2.62 \text{ g/cm}^3$  used by Reyment (1958), and Heptonstall (1970), whereas Westermann (1977) used  $2.60 \text{ g/cm}^3$ , and Ebel (1983) citing Collins et al. (1980) used a density of  $2.53 \text{ g/cm}^3$  for the entire shell. Variation of shell density within the shell was mentioned by Mutvei (1983) due to incorporation of different amounts of organic matter like conchiolin (Stenzel, 1964). Our own observation using a pycnometer results in  $2.57 \text{ g/cm}^3$  for the outer shell and  $2.51 \text{ g/cm}^3$  for septal shell material. It seems likely that there are slight variations of the organic content within the shell of one specimen, between different specimens of one species and between different specimens of different species.

It seems also likely that the density of fresh caught specimens is higher compared to recent shells from museum collections due to a higher amount of wet organic matter.

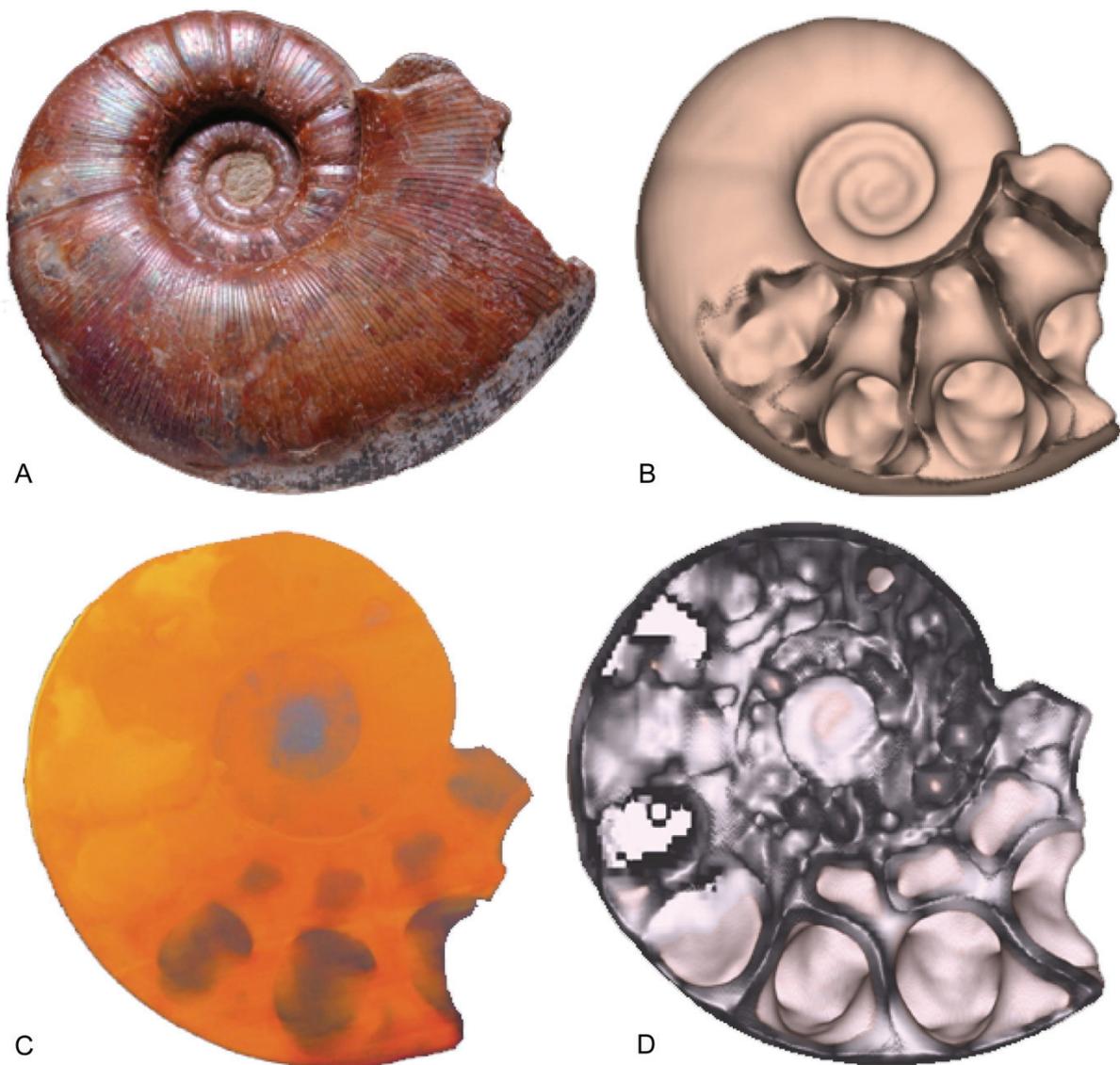
More difficulties occur for the calculation of the soft body (soft body in the body chamber, siphuncle, jaw apparatus, pellicle,) which is usually never recorded in fossils specimens.

The highest volume is captured by the cephalopod soft body within the body chamber. The mass of the soft body was calculated using the assumption that the volume of the soft body equals the volume of the body chamber, which is following Kröger (2002) surely too high.

However, due to the fact that the soft parts of the animal are only slightly heavier than seawater and given with  $1.026-1.068 \text{ g/cm}^3$  the impact of the total buoyancy is only marginal.

Transferring this method to fossil cephalopod material several other problems arise. During first tests it turned out that only the rare hollow preservation of ammonite shells is good enough for this purpose. It was observed that secondary calcite often found in ammonite fossil chambers has a similar density like the original shell material. That results in similar shade of grey and makes a sufficient distinction, needed for creating a 3D modell, impossible. The same holds true for sediment that filled up the ammonite chambers.

Finally, it occurs very often that the inner surface of the ammonite chambers were covered by a thin pyrite layer that originated due to the decomposition of the pellicle under dysoxic conditions. That pyrite layer resorbes the x-rays of the tomograph so that no data for this area are availbale (Fig. 3).



**Figure 3: Argonauticeras sp., Lower Albian, Madagascar about 7.5 cm in diameter. A: Photography. B: Ct-scan showing the secondary calcite covering the inner surface of the chambers masking minute details. C: Ct-scan showing most of the chambers being completely filled with sediment. D: Ct-scan indicating pyrite within one or two chambers readily identifiable due to the pixelated white areas inside the shell. All ct-scans from pre-scanning with 1mm voxelsize.**

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## References

- BANDEL, K. (1983): Wandel der Vorstellungen von der Frühevolution der Mollusken besonders der Gastropoda und Cephalopoda. *Paläontologische Zeitschrift* 57 (3-4), S. 271-284.
- COLLINS, D., WARD, P. D. (1980): Adolescent Growth and Maturity in *Nautilus* - In: *Nautilus*. SAUNDERS, W. B., LANDMAN, N. H. (eds.), S. 421-432, Plenum Press New York and London.
- DENTON, E. J., GILPIN-BROWN, J. B. (1961a): The Buoyancy of the Cuttlefish, *Sepia officinalis* (L.). *Journal of the marine biological Association, United Kingdom* 41, S. 319-364.
- DENTON, E. J., GILPIN-BROWN, J. B. (1961b): The distribution of gas and liquid within the cuttlebone (L.). *Journal of the marine biological Association, United Kingdom* 41, S. 365-381.
- DENTON, E. J., GILPIN-BROWN, J. B. (1966): On the buoyancy of the pearly *Nautilus*. *Journal of the marine biological Association, United Kingdom* 46, S. 723-759.
- DENTON, E. J., GILPIN-BROWN, J. B. (1971): Further Observations on the Buoyancy of *Spirula*. *Journal of the marine biological Association, United Kingdom* 46, S. 363-373.
- DENTON, E. J., GILPIN-BROWN, J. B., HOWARTH, J. V. (1961): The osmotic mechanism of the cuttlebone. *Journal of the marine biological Association, United Kingdom* 41, S. 351-364.
- DENTON, E. J., GILPIN-BROWN, J. B., HOWARTH, J. V. (1967): On the Buoyancy of *Spirula spirula*. *Journal of the marine biological Association, United Kingdom* 47, S. 181-191.
- DUNSTAN, A. J., WARD, P. D., MARSHALL, N. J. (2011): Vertical Distribution and Migration Patterns of *Nautilus pompilius*. *Plos One* 6 (2), S. 1-11.
- EBEL, K. (1983): Berechnungen zur Schwebfähigkeit von Ammoniten. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*. 1983 (10), S. 614-640.
- GREENWALD, L., COOK, C. B., WARD, P. D. (1982): The structure of the chambered *Nautilus* siphuncle: the siphuncular epithelium. *Journal of Morphology* 172, S. 5-22.
- HASZPRUNAR, G. (1996): The Mollusca: Coelomate turbellarians or mesenchymate annelids? – In: *Origin and Evolutionary Radiation of the Mollusca*. Taylor, J. (ed.), S. 1-28, Oxford University Press.
- HASZPRUNAR, G. (2000): Is the Aplacophoran monophyletic? A cladistic point of view. *American Malacology Bulletin* 15, S. 115-130.
- HEPTONSTALL, W. B. (1970): Buoyancy control in ammonoids. *Lethaia* 3, S. 317-328.
- HEWITT, R. A., WESTERMANN, E. G. (1993): Growth rates of ammonites estimated from aptychi. *Geobios, Memoire Special* 15, S. 203-208.

HOFFMANN, R. (2010): New insights on the phylogeny of the Lytoceratoidea (Ammonitina) from the septal lobe and its functional interpretation. *Revue de Paléobiologie* 29 (1), S. 1-156.

JACOBS, D. K. (1996): Chambered Cephalopod Shells, Buoyancy, Structure and Decoupling: History and Red Herrings. *Palaios* 11, S. 610-614.

KORN, D., KLUG, C. (2007): Conch Form Analysis, Variability, Morphological Disparity, and Mode of Life of the Frasnian (Late Devonian) Ammonoid *Manticoceras* from Coumiac (Montagne Noire, France) – In: *Cephalopods Present and Past – New Insights and Fresh Perspectives*. LANDMAN, N. H., DAVIS, R. A., MAPES, R. H. (eds.), S. 57-85, Springer Verlag.

KRÖGER, B. (2002): On the efficiency of the buoyancy apparatus in ammonoids: evidences from sublethal shell injuries. *Lethaia* 35, S. 61-70.

KRUTA, I., LANDMAN, N., ROUGET, I., CECCA, F., TAFFOREAU, P. (2011): The Role of Ammonites in the Mesozoic Marine Food Web Revealed by Jaw Preservation. *Science* 331, S. 70-72.

LEHMANN, W. M. (1932): Stereo-Röntgenaufnahmen als Hilfsmittel bei der Untersuchung von Versteinerungen. *Natur und Museum* 62, S. 323-330.

LONGRIDGE, L. M., SMITH, P. L., RAWLINGS, G., KLAPTOCZ, V. (2009): The impact of asymmetries in the elements of the phragmocone of early Jurassic ammonites. *Palaeontologia Electronica* 12 (1A), S. 1-15.

MOSELEY, H. (1838): On the geometrical forms of turbinated and discoid shells. *Philosophical Transactions of the Royal Society* 1838, S. 351-370.

MUTVEI, H., REYMENT, R. A. (1973): Buoyancy control and siphuncle function in ammonoids. *Palaeontology* 16, S. 623-636.

RAUP, D. M., CHAMBERLAIN, J. A. jr. (1967): Equations for volume and center of gravity in ammonoid shells. *Journal of Paleontology* 41 (3), S. 566-574.

REYMENT, R. A. (1958): Some factors in the distribution of fossil Cephalopods. *Acta Universitatis Stockholmiensis - Stockholm Contributions in Geology* 1, S. 97-184.

REYMENT, R. A. (1973): Factors in the distribution of fossil cephalopods. Part 3: Experiments with exact models of certain shell types. *Bulletin of the Geological Institute of the University of Uppsala* N. S. 4, S. 7-41.

SEILACHER, A., LABARBERA, M. (1995): Ammonites as Cartesian Divers. *Palaios* 10, S. 493-506.

STENZEL, H. B. (1964): Living *Nautilus* – In: *Treatise on Invertebrate Paleontology Part K Mollusca 3: Cephalopoda-Generell Features-Endoceratoidea-Actinoceratoidea-Nautiloidea-Bactritoidea*. Moore, R. C. (ed.), S. K59-K93.

STUERMER, W. (1970): Soft parts of Cephalopods and Trilobites: Some Surprising Results of X-Ray Examinations of Devonian Slates. *Science*, New Series 170 (No. 3964), S. 1300-1302.

TRUEMAN, A. E. (1941): The ammonite body chamber with special reference to the buoyancy and mode of life of the living ammonite. *Quaternary Journal of the Geological Society of London* 96, S. 339-383.

WARD, P. D. (1980): Restructuring the chambered *Nautilus*. *Paleobiology* 6 (3), S. 247-249.

WARD, P. D. (1987): The natural history of *Nautilus*. 267 Seiten, Allen and Unwin, Winchester.

WARD, P. D., MARTIN, A. W. (1978): On the buoyancy of the pearly *Nautilus*. *Journal of Experimental Zoology* 205, S. 5-12.

WELLS, M. (1990): The dilemma of the jet set. *The New Scientist Issue* 1704, S. 44-47.

WESTERMANN, G. E. G. (1977): Form and function of orthoconic cephalopod shells with concave septa. *Paleobiology* 3 (3), S. 300-321.