学位論文（要約）

Evolution and diversity of biomineralogical nature in ectocochleate cephalopod septa

（外殻性有殻頭足類の隔壁における結晶学的性質の進化と多様性）

平成 28 年 12 月博士（理学）申請

東京大学大学院理学系研究科

地球惑星科学専攻

竹田　裕介

Abstract

Septa, characteristic structures of ectocochleate cephalopods, enable ammonoids and nautiloids to gain buoyancy and swimming ability by restoring low-pressure gas in the phragmocone. The macro-morphological differences in septa between ammonoids and nautiloids have been intensively examined, and their functionality and morphogenetic mechanisms have been well discussed. However, little attention has been paid to their biomineralogical nature; the septa in these two groups are regarded to be biomineralogically homologous. Determination of biomineralogical differences is essential for recognizing the functional morphology and morphogenesis of the septa and their major evolutionary events such as extension of their habitat by buoyancy and swimming ability, ammonoid extinction and nautiloid survival in the K/Pg boundary, and biomineralization process of structures unique to cephalopods.

This study conducted comparative crystallographic analyses on the nacreous structure of ectocochleate cephalopod septa. The crystallographic orientation pattern, (crystallographic texture) and microstructure (morphology and mode of layering of the constituent polycrystalline materials) of the septa were analyzed and compared with a focus on the effects by phylogeny and habitat environments.

In Chapter 1, as an introduction, macro-morphological diversity of ectocochleate cephalopod septa and its functional morphology are reviewed. Then, the significance of biomineralogical properties for the elucidation of functional morphology of septa is mentioned.

In the study described in Chapter 2, the septa of extant nautiloid individuals such as *Nautilus pompilius*, *N. belauensis*, *N. macromphalus*, and *Allonautilus scrobiculatus* from various geographic localities including the Philippines, Fiji, Palau, New

Caledonia, and Indonesia in addition to those raised in an aquarium were analyzed by using X-ray diffraction (XRD) to determine their crystallographic textures. The {002}, {012}, {102}, {112} pole figures generated from the diffracted pattern reveals that, in general, the septa are composed of aragonitic polycrystals with their *c*-, *a*-, and *b*-axes perpendicular to the septal surface, parallel to the dorsoventral direction, and parallel to the left-right direction, respectively. These characteristics indicate an ordered texture. However, deviations from the ordered texture also exist in the *a*- and *b*-axes directions, showing a slightly disordered texture. The degree of deviation was measured on the basis of the full width half maximum (FWHM) values calculated from the {012} pole figures. Combining the *c*-axis orientation indicated by {002} pole figures, two FWHM values in the {012} pole figures were utilized as indices of *a*- and *b*-axes misalignment. As a result, variability in *a*- and *b*-axes misalignment in septal aragonitic polycrystals among individuals was revealed. They were constant in each septum and submature–matured septa in each individual. Moreover, individuals from the same phylogeographic group shared similar FWHM values. In this study, the relationship of larger FWHM values with a markedly disordered crystallographic texture and a shallower-habitat phylogenetic group is reported for the first time. The investigation on aquarium-raised individuals confirmed that sea water pressure does not abiotically affect the crystallographic texture. These results suggest that the crystallographic texture of the recent nautilid septa are influenced genetically and reflect certain adaptive significance toward their habitat water depth. Moreover, the crystallographic texture analysis of the septa is relevant to the elucidation of phylogeographic relationships of recent nautilids.

In the study described in Chapter 3, the microstructural analyses on recent nautilid septa were conducted qualitatively and quantitatively. The nautilid septa are known to be composed entirely of nacreous structures. In this study, the morphology and mode of layering of the tablets that construct the nacreous structure were examined and measured by using scanning electron microscopy and synchrotron X-ray nano computed tomography. As a result, the recent nautilid septal nacre is characterized by a laterally long, thin, and elongated hexagonal shape. These tablets are stacked in a columnar fashion in a broad view as reported in previous studies. However, the columns are not continuous throughout the septa; rather, they are often separated in two columns that in some cases fuse into one column. Observations of the concave septal surface revealed that such a mode of layering is achieved by tablets growing on the margins of the underlying tablets. In addition, the elongated hexagonal tablets are well aligned with each other, and “twinning” is often present. Along with the crystallographic texture investigated in Chapter 1, the *a*-axis of the nacreous tablet is parallel to the elongated direction of the tablets. The nautilus septal nacre is similar to that of pinnid and nuculid bivalves, which has been previously described as a row-stack nacreous structure. Because the nautilus septal nacre is regarded as a having a columnar nacreous structure, which is also observed in gastropod nacre, this finding is important in comparative studies of molluscan nacreous structures. The measurements of nacreous tablets revealed no distinct variation in the septal nacre of recent nautilus belonging to different phylogeographic groups.

In Chapter 4, fossil ectocochleate cephalopod septa were compared with those of recent nautilids examined in the previous chapters. Co-occurring species of ammonoids and nautiloids with similar habitat depth were utilized to exclude the influence of habitat environment on the septal biomineralogical properties. The examined specimens include the Upper Cretaceous nautiloid *Eutrephoceras*, scaphitid ammonoid

Hoploscaphites nodosus, and *H. brevis* from the western interior province of North America in addition to the Lower Cretaceous nautiloid *Cymatoceras* sp. and douvilleiceratid *Douvilleiceras* sp. from Madagascar. The fossil nautiloids show crystallographic textures and microstructures similar to those in recent samples, i.e., *a*-axis parallel to the vertical direction and *b*-axis parallel to the left-right direction, although the degree of misalignment was greater in the fossils. The sizes of the tablets in the fossil nautiloids are within the same range as those of the recent specimens. However, the tablet stacks clearly show a columnar fashion. The examined fossil species are considered to have had shallower habitats. Considering the fossil record of nautiloids, it is suggested from a biomineralogical perspective that the septa and their formation process have been conservative since the early Mesozoic; however, the crystallographic misalignment and mode of layering of the nacreous tablets might reflect their variable habitat depth. In contrast, the ammonoid septal nacre shows polygonal tablets with thicknesses similar to those of the nautiloids. Moreover, although their crystallographic texture shows a *c*-axis perpendicular to the septal surface, as in the nautiloids, it is completely disordered in *a*- and *b*-axes, which are represented by ring-like pole figures in the {012}, {102}, and {112} planes. This result suggests that the crystallographic properties of ectocochleate septa, including their crystallographic orientation and nacreous structure, are conservative at the subclass level. However, they might vary considerably between the Ammonoidea and the Nautiloidea, which developed different septal morphologies.

In Chapter 5, these new insights are discussed for understanding the evolution of ectocochleate septa, particularly from aspects of morphogenesis and functional morphology. The similarity of the crystallographic properties of nautiloid septa to the bivalves suggests a terrace-like formation of nacre. The alignment of tablet elongation and crystallographic ordering in bivalves are explained by geometric selection based on the faster growth along in the *b*-axis of aragonite than that along in the *a*-axis. Such crystal growth due to the geometric selection might occur in nautiloid septal nacre, because their nacreous tablets are also elongated. However, the elongation direction and crystallographic orientation is inconsistent with those of bivalves. The mechanisms for the vertical stacking of the nautiloid septal nacreous tablet through the interlamellar membranes would be similar to those of bivalves because the similar mode of tablet layering indicates the existence of mineral bridges produced by rupture owing to permeability pressure.

Contrary to the bivalve-like nautiloid nacre, the ammonoid columnar nacreous structure, which is similar to the "stack of coins" structure in gastropods, can be considered to have formed by mineral bridges located in the central area of the tablets. The completely disordered crystallographic orientation pattern of the ammonoid septal nacre is consistent with such a gastropod-like nacre growth mechanism, suggesting that weak or no competition/interaction with lateral adjacent tablets/columns. These differences in formation mechanisms for nautiloid and ammonoid septa indicate that different morphogenetic constraints might exist in their septal formations, which affect the macro-morphological difference of septa, based on the different properties and dynamics of the septal mantle and the septal mantle epithelium.

The nacreous structure is known to be mechanically excellent among molluscan shell microstructures. Therefore, the development of the nacreous structure in septa would be reasonable to resist high pressure in the ambient surrounding water because low-pressure gas fills the phragmocone. However, whether or not the nacreous structure is mechanically optimized and performs best depends on the constituent tablet size and its mode of layering. In this respect, the mechanical performances and optimization of both nacreous tablets, particularly the lateral and overlap length, were compared by using a multi-objective optimization model. The results indicate that the tablet and overlap aspect ratios of the nautiloids are close to the optimal values to perform high tensile strength, stiffness, and toughness. On the contrary, the septal nacreous tablets of the ammonoids are short in lateral and overlap lengths toward the thickness, suggesting that they are not optimized in these mechanical properties. This thesis revealed not only the difference in the mechanical properties of septa, but also the anisotropic characteristics of septa, especially in nautiloids. Such anisotropy of the septa necessitates reconsideration of its functional macro-morphology, because previous numerical analyses on the septal macro-morphology have been assumed the isotropy of the septal material. This study demonstrates for the first time, that the biominelogical studies on ectocochleate cephalopod septa is important not only for biomineral research itself, but also important to understand the evolution and ecology of macro-morphology of septa.

This thesis suggests that the gastropod- and bivalve-type nacre formation mechanisms themselves are not different because the both types are present in the ectocochleate cephalopod septa. The septa are flexible and continuous according to their habitat environments, although the genetic and evolutionary origin might not be homologous among mollusks. Moreover, it is suggested that extremely subtle differences in the crystallographic structure in genus, species, and individual levels should be considered.

Contents

Chapter 1: General introduction 2
Chapter 2: Variability in the crystallographic texture of recent ectocochleate cephalopod septa 8
- **Introduction** 8
- **Materials** 9
- **Methods** 20
- **Results** 24
- **Discussion** 45
- **Conclusion** 51

Chapter 3: Nacreous structure of recent ectocochleate cephalopod septa and variability in nacreous tablet morphology 53
- **Introduction** 53
- **Materials** 54
- **Methods** 55
- **Results** 57
- **Discussion** 72
- **Conclusions** 81

Chapter 4: Microstructural and crystallographic properties of fossil nautiloids and ammonoids: case studies from the Upper Cretaceous of U.S. Western Interior and the Lower Cretaceous of Madagascar 82
- **Introduction** 82
- **Materials and geological settings** 83
- **Methods** 86
- **Results** 87
- **Discussion** 101
- **Conclusions** 109

Chapter 5: General discussion 110
Summary 127
Acknowledgments 129
References 131

Chapter 1: General introduction

The appearance of marine organisms has radiated in various environments including differences in water depth, temperature, and bottom sediments through the Phanerozoic (e.g., Bush and Bambach, 2011). Such diversification and evolutionary trends are importants topic in evolutionary paleobiology. Hard tissues of organisms, such as molluskan shells, are clues to elucidate the trends from past to present.

Mollusks in oceans have greatly diversified since the Paleozoic. Most are benthic and have adapted to various sea bottom conditions. However, the cephalopod has a developed swimming ability, and their presence has radiated horizontally and vertically in oceans. Among them, externally shelled (ectocochleate) and internally shelled (endocochleate) cephalopods acquired chambered shells as a hydrostatic apparatus. Inside the shells of ectocochleate cephalopods, the septa separate the body chamber and the phragmocone, which is a space filled with low-pressure gas. Studies have revealed that modern chambered cephalopods *Nautilus*, *Sepia*, and *Spirula* maintain neutral buoyancy with the aid of low-pressure gas within the phragmocone (Denton and Gilpin-Brown, 1966, 1973; Gilpin-Brown, 1972).

On the basis of essential similarity in overall shell shape, ammonoids, an extinct group of ectocochleate cephalopods, are considered to have maintained neutral buoyancy in the same manner as that of the modern *Nautilus* (Trueman, 1940; Denton and Gilpin-Brown, 1966; Gilpin-Brown, 1972; but see Shigeta (1993) for the negative buoyancy hypothesis). However, the morphology of the septa differs significantly between nautiloids and ammonoids. In general, nautiloids have synclastically corrugated septa showing an adapically convexed bowl-like shape, whereas ammonoids have anticlastically corrugated septa that are frequently folded to form complex suture lines at their connection to the inner surface of the shell wall (e.g., Klug et al., 2015; Inoue and Kondo, 2016). During the evolution of ammonoid phylogeny from the Early Devonian to the end of the Cretaceous, the complicated septal morphology evolved repeatedly (Klug et al., 2015, and references therein).

Although effective macro-morphological studies of ectocochleate cephalopod septa exist, our knowledge of their micro-scale architecture and its evolutionary significance is considerably insufficient, preventing the elucidation of the septal evolution from the aspect of morphogenesis and functional morphology. For example, several studies attempted to explain the formation of the complex morphology of the septa from the perspective of deformation and dynamics of the septal mantle (e.g., Seilacher, 1973, 1975; García-Ruiz et al., 1990; García-Ruiz and Checa, 1993; Checa and Garcia-Ruiz, 1996; Klug and Hoffmann, 2015; Inoue and Kondo, 2016) and morphogen diffusion (Hammer, 1999). However, the mechanism for carbonate crystals growth and stacking to form septal shell material remains unknown as are variation in crystallographic characteristics. Moreover, considering the main function of the septa as a hydrostatic organ and the presence of low-pressure gas in the phragmocone, the ammonoid septa must have possessed sufficient mechanical strength to withstand ambient high water pressure such as that demonstrated by the recent *Nautilus*. On the basis of this hypothesis, several attempts have been made to estimate the mechanical advantage of ammonoid septa by using numerical analysis (i.e., finite element analysis; Hewitt and Westermann, 1987; Hewitt et al., 1989, 1993; Daniel et al., 1997; Hassan et al., 2002; Lemanis et al., 2016). Although such attempts are helpful for understanding the three-dimensional complex septal morphology, data of the physical properties of the examined material is necessary to conduct such analysis. Previous studies examining ammonoid septal strength have assumed that the mechanical properties of the septa are identical to that of recent molluscan shells and they are isotoropic (Daniel et al., 1997; Hassan et al., 2002; Lemanis et al., 2016). However, the physical properties are highly variable among molluscan shells depending on the microstructural architecture (e.g., Currey, 1988; Vincent, 2001; Sun and Bhushan, 2012). Moreover, the prevous studies treating the functional macro-morphology of septa ignored the anisotropy of the shell material, although it might influence on their physico-mathematical analyses. Therefore, detailed analysis and comparison of the crystallographic properties and anisotropy of cephalopod septa are required to address their mechanical advantage.

The purpose of this thesis is to discuss the diversity and evolution of the septa of ectocochleate cephalopods from the aspect of their crystallographic properties. Molluscan shells are composed mainly of calcium carbonate polycrystalline materials of calcite or aragonite. This thesis focuses on two biomineralogical properties, crystallographic texture and shell microstructure, both of which can be analyzed even in fossils. The former represents the three-dimensional distribution of the crystallographic axes. It is compared and analyzed as pole figures, which represents the distribution of crystals projected in two-dimensional plots in the equatorial plane (Fig. 1.1). The latter represents the shape, size and mode of layering of biomineralogical materials (Fig. 2.2). Previously, both of the biomineralogical properties have provided various insight in the evolution and ecology of molluscan shells including phylogenetic relationships (e.g., MacClintock 1967; Taylor et al., 1969; Hedegaard and Wenk, 1998; Chateigner et al., 2000, 2010; Frýda et al., 2009, 2010; Génio et al., 2012; Sato et al., 2013; Sato and Sasaki, 2015), crystal growth and shell formation (e.g., Ubukata, 1994; Checa, 2000; Checa and Navarro, 2001, 2005; Checa et al., 2005, 2006; Nudelman et al., 2006;

Fig. 1.1
インターネット公表に関する同意が得られなかったため非公表

Nudelman, 2015; Gilbert et al., 2008, 2012; Olson et al., 2013), and ecology and functional significance (e.g., Wada, 1972; Currey, 1988; Vincent, 1999; Nishida et al., 2012, 2015; Olson et al., 2012; Olson and Gilbert, 2012; Rousseau and Rollion-Bard, 2012).

In this thesis, at first, the crystallographic textures of recent nautilid septa are examined to estimate their variation and genetic relationships in Chapter 2. In Chapter 3, the shell microstructure of the recent nautilid septa and the polycrystalline shape are described to reveal the mode of layering in comparison with the variation in crystallographic texture. In Chapter 4, the crystallographic textures and the shell microstructures of fossil nautiloids and ammonoids are compared to reveal the differences in crystallographic properties among these two different subclasses. Finally, in Chapter 5, the significance of diversity regarding the crystallography and microstructural morphology of the septa among ectocochleate cephalopods with various forms of septate shells is discussed on a macroscopic scale.

Fig. 1.1 (page 5). Examples of crystallographic textures of recent bivalve and gastropod nacreous structure. (A) Some crystal planes of aragonite and the stereographic projection of a crystal plane onto the equatorial plane ((011) in the example). (B–E) Pole figures based on EBSD analyses (B–D) and XRD analysis (E). For all pole figures, the shell surfaces are parallel to the equatorial planes and the growth directions are left to right. (B) Pteriid bivalve *Pteria hirundo*. The analysis was demonstrated on the nacreous structure near the outer prismatic structure. (C) Mytilid bivalve *Modiolus barbatus*. (D) Haliotid gastropod *Haliotis asinina*. (E) Turbinid gastropod *Bolma rugosa*. These pole figures suggest that, in these species, the *c*-axis of aragnitic nacreous polycrystals are aligned perpendicular to the shell surface, but the alignment pattern in *a-b* planes is variable among species. Modified from: (B) Checa et al. (2006, fig. 2b); (C) Frýda et al. (2010, fig. 6A–C); (D) Frýda et al. (2009, fig. 4D–F); (E) Checa et al. (2009a, Fig. S2b).

Fig. 1.2
インターネット公表に関する同意が得られなかったため非公表

Fig. 1.2. Examples of nacreous structures of recent bivalves and gastropods. (A, B) Sheet nacreous structure. (C) Lenticular (sheet) nacreous structure. (D) Row-stack (sheet) nacreous structure. (E, F) Columnar nacreous structure. (A) Apertural inner shell surface of pteriid bivalve *Pinctada radiata*. (B) Radial section of inner layer of nuculid bivalve *Acila mirabilis*. Arrow indicates the growth direction. (C) Fractured cross section of unionid bivalve *Leptodea fragilis*. (D) Depositional surface of pinnid bivalve *Atrina rigida*. (E) Apertural inner shell surface of pleurotomariid gastropod *Perotrochus caledonicus*. (F) Fractured cross section of trochid gastropod *Trochus niloticus*. Modified from: (A) Wise (1970b, Plate 1, Fig. 1); (B) Sato and Sasaki (2015, Fig. 39); (C) Frýda et al. (2010, Fig. 3B); (D) Carter et al. (2012, Fig. 267); (E) Checa et al. (2009, Fig. 1); (F) Bruet et al. (2005, Fig. 4).

Chapter 2: Variability in the crystallographic texture of recent ectocochleate cephalopod septa

第 2 章

本章については、5 年以内に雑誌などで刊行予定のため、非公開。

Chapter 3: Nacreous structure of recent ectocochleate cephalopod septa and variability in nacreous tablet morphology

第 3 章
本章については、5 年以内に雑誌などで刊行予定のため、非公開。

Chapter 4: Microstructural and crystallographic properties of fossil nautiloids and ammonoids: case studies from the Upper Cretaceous of U.S. Western Interior and the Lower Cretaceous of Madagascar

第 4 章

本章については、5 年以内に雑誌などで刊行予定のため、非公開。

Chapter 5: General discussion

第 5 章

本章については、5 年以内に雑誌などで刊行予定のため、非公開。

Summary

This thesis attempted comparative crystallographic analysis on the septal nacreous structures of ectocochleate cephalopods including nautiloids and ammonoids, which were treated as structurally homologous microstructures in previous research. The nautiloid septal nacre is characterized by strong anisotropy, which is laterally long, thin tablets stacked in a row-stack manner. The crystallographic texture of this nacre shows also anisotropy. It has an ordered pattern, such that the *a*-axis is parallel to the vertical direction, the *b*-axis is parallel to the horizontal direction, and the *c*-axis is perpendicular to the septal surface. The degree of disorientation in the *a*- and *b*-axes reflects the phylogeographically separated genetic populations of recent species, which might be applicable to the fossil linages. The ammonoid septal nacre is characterized by laterally short tablets stacked in columns. The crystallographic texture of this nacre shows an unordered pattern such that the *a*- and *b*-axes are random and the *c*-axis is perpendicular to the septal surface.

The mode of layering of the nacreous tablets, crystallographic texture, and inferred nacre-formation mechanisms suggest similarities in nautiloid and bivalve nacres and in ammonoid and gastropod nacres. The coexistence of both bivalve-type row-stack nacre and gastropod-type columnar nacre in ectocochleate cephalopod linages suggests variability and diversity in the crystallographic properties of septal nacre and in the morphogenetic constraints. From the functional morphological aspect of septa as a hydrostatic organ, the nautiloid nacreous tablets are much more mechanically optimized against the tensile strength than those of ammonoids.

The anisotropic biomineralogical properties of septal nacre is not negligible for the material properties. Moreover, functional macro-mophological septal analysis also must

consider such anisotropic material of the septa. Therefore, investigation of biomineralogical properties of ectocochleate cephalopod septa is necessary to understand the ecology, evolution, and functional morphology of septa, from both aspects of macroscopic and microscopic views. In addition, biomoineralogical diversity and evolution of septal nacre revealed in this thesis also suggest the importance of structural comparison of nacreous structures on lower taxonomic levels for a better understanding of their evolution, homology, and morphogenesis.

Acknowledgments

I greatly appreciate Associate Prof. Takenori Sasaki (UMUT) for his supervision and fruitful discussion throughout the study. I also appreciate Emeritus Prof. Kazushige Tanabe (The University of Tokyo; UT) for his encouragement and providing me valuable *Nautilus* specimens. I also thank Prof. Kazuyoshi Endo, Prof. Toshihiro Kogure, Dr. Takanobu Tsuihiji (all UT), and Associate Prof. Takao Ubukata (Kyoto University) for their critical comments on this thesis. Toba Aquarium (Toba, Mie Prefecture, Japan) kindly providing reared individuals of nautilids. I also grateful to Mr. Fumiya Moritaki (Toba Aquarium) for the discussion on the aquarium reared individuals. Dr. Taizo Shima (Nihon Ayeaye Fund) kindly provided me fossil specimens from Madagascar. Mr. Jamie Brezina and Mr. Neil Larson assisted my sample collection in South Dakota, USA. Dr. Yasuhiro Ito (UMUT) kindly assisted me to analyze the specimens housed in UMUT. Associate Prof. Hyuma Masu (Chiba University) is acknowledged for helping me with XRD experiments. The synchrotron radiation experiment was performed at the beamline BL47XU of SPring-8 with the approval of the Japan Synchrotron Radiation Research Institute (JASRI) (Proposal No. 2015B1837 and 2016A1711). Special thanks are due to Drs. Kentaro Uesugi, Akihisa Takeuchi, and Masato Hoshino (all in Japan Synchrotron Radiation Research Institute) for helping me with synchrotron radiation nano-CT experiments. Associate Prof. Akira Miyake and Mr. Yohei Igami (Kyoto University) kindly allowed me to use FIB-SEM to prepare the samples for synchrotron radiation experiment. Ms. Yu Maekawa (UMUT) helped me with SEM observations. I thank members in Evolutionary Paleobiology Seminar in UT for their critical discussions on my study. Especially, I appreciate Drs. Yasuhiro Iba (Hokkaido University), Kozue Nishida (National Institute of Technology, Ibaraki

College), and Kei Sato (Kanazawa University) for their fruitful discussion. I also thank the staff in UMUT for their museum administration. This study was supported in part by JSPS KAKENHI Grant Numbers JP16J06269 and Fukada Grant-in-Aid in 2015 by Fukada Geological Institute (Tokyo, Japan).

References

Addadi, L., Joester, D., Nudelman, F., Weiner, S. 2006. Mollusk shell formation: A Source of new concepts for understanding biomineralization processes. Chemistry – A European Journal 12, 980–987.

Addadi, L., Weiner, S., 1997. A pavement of pearl. Nature 389, 912–915.

Alvarez-Lloret, P., Rodriguez-Navarro, A.B., Checa, A.G., 2008. Evolution of the microstructure and crystallographic orientation during shell growth in *Psilunio littoralis* and *Nautilus belauensis*. Mineralogical Magazine 72, 163–167.

Arkell, W.J., Kummel, B., Wright, C.W., 1957. Mesozoic Ammonoidea. in: Arkell, W.J., Furnish, W.M., Kummel, B., Miller, A.K., Moore, R.C., Schindewolf, O.H., Sylvester-Bradley, P.C., Wright, W.C. (Eds.), Treatise on Invertebrate Paleontology, Part L, Mollusca 4. The University of Kansas Press, Lawrence, Kansas, pp. L80–L490.

Arnold, J.M., 1985. Shell growth, trauma, and repair as an indicator of life history for *Nautilus*. Veliger 27, 386–396.

Bandel. K., 1977. Übergange von der Perlmutter-Schicht zu prismatischen Schichttypen bei Mollusken. Biomineralisation Forschungsberichte 9, 28–47.

Bandel, K., 1979. The nacreous layer in the shells of the gastropod-family Seguenziidae and its taxonomic significance. Biomineralisation Forschungsberichte 10, 49–61.

Bar-On, B., Wagner, H.D., 2013. Structural motifs and elastic properties of hierarchical biological tissues – A review. Journal of Structural Biology 183, 149–164.

Barthelat, F., 2014. Designing nacre-like materials for simultaneous stiffness, strength and toughness: Optimum materials, composition, microstructure and size. Journal of the Mechanics and Physics of Solids 73, 22–37.

Barthelat, F., Dastjerdi, A.K., Rabiei, R., 2013. An improved failure criterion for biological and engineered staggered composites. Journal of The Royal Society Interface 10, 20120849.

Barthelat, F., Li, C.-M., Comi, C., Espinosa, H.D., 2006. Mechanical properties of nacre constituents and their impact on mechanical performance. Journal of Materials Research 21, 1977–1986.

Barthelat, F., Tang, H., Zavattieri, P.D., Li, C.-M., Espinosa, H.D., 2007. On the mechanics of mother-of-pearl: A key feature in the material hierarchical structure. Journal of the Mechanics and Physics of Solids 55, 306–337.

Bonacum, J., Landman, N.H., Mapes, R.H., White, M.M., White, A.-J., Irlam, J., 2011. Evolutionary radiation of present-day *Nautilus* and *Allonautilus*. American Malacological Bulletin 29, 77–93.

Bonnaud, L., Ozouf-Costaz, C., Boucher-Rodoni, R., 2004. A molecular and karyological approach to the taxonomy of *Nautilus*. Comptes Rendus Biologies 327, 133–138.

Bruet, B.J.F., Qi, H.J., Boyce, M.C., Panas, R., Tai, K., Frick, L., Ortiz, C., 2005. Nanoscale morphology and indentation of individual nacre tablets from the gastropod mollusc *Trochus niloticus*. Journal of Materials Research 20, 2400–2419.

Bush, A.M., Bambach, R.K., 2011. Paleoecologic megatrends in marine metazoa. Annual Review of Earth and Planetary Sciences 39, 241–269.

Carlson, B.A., 1987. Collection and aquarium maintenance of *Nautilus*. in: Saunders, W.B., Landman, N.H. (Eds.), *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York, 563–583.

Carter, J.G., 1990a. Skeletal biomineralization: patterns, processes and evolutionary trends. Volume I. Van Nostrand Reinhold, New York.

Carter, J.G., 1990b. Skeletal biomineralization: patterns, processes and evolutionary trends. Volume II. Van Nostrand Reinhold, New York.

Carter, J.G., Clark II.G.R., 1985. Classification and phylogenetic significance of molluscan shell microstructure. University of Tennessee Department of Geological Sciences Studies in Geology 13, 50–71.

Carter, J.G., Harries, P.J., Malchus, N., Sartori, A.F., Anderson, L.C., Bieler, R., Bogan, A.E., Coan, E.V., Cope, J.C.W., Cragg, S.M., García-March, J.R., Hylleberg, J., Kelley, P., Kleemann, K., Kříž, J., Mcroberts, C., Mikkelsen, P.M., Pojeta, J., Tëmkin, I. Jr., Yancey, T., Zieritz, A., 2012. Part N, Revised, Volume 1, Chapter 31: Illustrated Glossary of the Bivalvia.Illustrated glossary of the Bivalvia. Treatise Online 48, 1–209.

Cartwright, J.H.E., Checa, A.G., 2007. The dynamics of nacre self-assembly. Journal of The Royal Society Interface 4, 491–504.

Cartwright, J.H.E., Checa, A.G., Escribano, B., Sainz-Diaz, C,I., 2009. Spiral and target patterns in bivalve nacre manifest a natural excitable medium from layer growth of a biological liquid crystal. PNAS 106, 10499–10504.

Chateigner, D., Hedegaard, C., Wenk, H.-R., 2000. Mollusc shell microstructures and crystallographic textures. Journal of Structural Geology 22, 1723–1735.

Chateigner, D., Ouhenia, S., Krauss, C., Hedegaard, C., Gil, O., Morales, M., Lutterotti, L., Rousseau, M., Lopez, E., 2010. Voyaging around nacre with the X-ray shuttle: From bio-mineralisation to prosthetics via mollusc phylogeny. Materials Science and Engineering A 528, 37–51.

Checa, A., 2000. A new model for periostracum and shell formation in Unionidae (Bivalvia, Mollusca). Tissue & Cell 32, 405–416.

Checa, A.G., Cartwright, J.H.E., Willinger, M.-G., 2009b. The key role of the surface membrane in why gastropod nacre grows in towers. PNAS 106, 38–43.

Checa, A.G., Cartwright, J.H.E., Willinger, M.-G., 2011. Mineral bridges in nacre. Journal of

Structural Biology 176, 330–339.

Checa, A.G., Garcia-Ruiz, J.M., 1996. Morphogenesis of the septum. in: Landman, N.H., Tanabe, K., Davis, R.A., (Eds.), Ammonoid paleobiology. Plenum, New York, pp. 253–296.

Checa, A.G., Mutvei, H., Osuna-Mascaó, A,J., Bonarski, J.T., Faryna, M., Berent, K., Pina, C.M., Rousseau, M., Macías-Sánchez, E., 2013. Crystallographic control on the substructure of nacre tablets. Journal of Structural Biology 183, 368–376.

Checa, A.G., Okamoto, T., Ramírez, J., 2006. Organization pattern of nacre in Pteriidae (Bivalvia: Mollusca) explained by crystal competition. Proceedings of the Royal Society B 273, 1329–1337.

Checa, A.G., Ramírez-Rico, J., González-Segura, A., Sánchez-Navas, A., 2009a. Nacre and false nacre (foliated aragonite) in extant monoplacophorans (=Tryblidiida: Mollusca). Naturwissenschaften 96, 111–122.

Checa, A.G., Rodríguez-Navarro, A., 2001. Geometrical and crystallographic constraints determine the self-organization of shell microstructures in Unionidae (Bivalvia: Mollusca). Proceedings of the Royal Society of London B 268, 771–778.

Checa, A.G., Rodríguez-Navarro, A.B., 2005. Self-organisation of nacre in the shells of Pterioida (Bivalvia: Mollusca). Biomaterials 26, 1071–1079.

Checa, A.G., Rodríguez-Navarro, A.B., Esteban-Delgado, F.J., 2005. The nature and formation of calcitic columnar prismatic shell layers in pteriomorphian bivalves. Biomaterials 26, 6404–6414.

Cobban, W.A., Walaszczyk, I., Obradovich, J.D., McKinney, K.C., 2006. A USGS zonal table for the Upper Cretaceous Middle Cenomanian-Maastrichtian of the Western Interior of the United States based on ammonites, inoceramids, and radiometric ages. U.S. Geological Survey Open-File Report 2006–1250, p. 45.

Cochran, J.K., Landman, N.H., Turekian, K.K., Michard, A., Schrag, D.P., 2003. Paleoceanography of the Late Cretaceous (Maastrichtian) Western Interior Seaway of North America: evidence from Sr and O isotopes. Palaeogeography, Palaeoclimatology, Palaeoecology 191, 45–64.

Collignon, M., 1963. Atlas des fossils caractéristiques de Madagascar (Ammonites), Albian. Service Géologique Tananariver, 10, 1–184.

Collins, D., Ward, P.D., 1987. Adolescent growth and maturity in *Nautilus*. in: Saunders, W.B., Landman, N.H. (Eds.), *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York, 421–432.

Crenshaw, M.A., Ristedt, H., 1975. Histochemical and structural study of nautiloid septal nacre. Biomineralisation Forschungsberichte 8, 1–8.

Currey, J.D., 1976. Further studies on the mechanical properties of mollusc shell material. Journal of Zoology, London 180, 445–453.

Currey, J.D., 1988. Shell form and strength. in: Trueman, E.R., Wilbur, K.M., Clarke, M.R., (Eds.) The Mollusca vol. 11: Form and function. Academic Press, New York, 183–210.

Dalbeck, P., England, J., Cusack, M., Lee, M.R., and Fallick, A.E., 2006. Crystallography and chemistry of the calcium carbonate polymorph switch in *M. edulis* shells. European Journal of Mineralogy, 18, 601–609.

Daniel, T.L., Helmuth, B.S., Saunders, W.B., Ward, P.D., 1997. Septal complexity in ammonoid cephalopods increased mechanical risk and limited depth. Paleobiology 23, 470–481.

Dauphin, Y., 2001. Nanostructures de la nacre des tests de céphalopodes actuels. Paläontologische Zeitschrift 75, 113–122.

Dauphin, Y., 2002. Fossil organic matrices of the Callovian aragonitic ammonites from Lukow (Poland): location and composition. International Journal of Earth Sciences 91, 1071–1080.

Dauphin, Y., 2006. Structure and composition of the septal nacreous layer of *Nautilus macromphalus* L. (Mollusca, Cephalopoda). Zoology 109, 85–95.

Dennis, K.J., Cochran, J.K., Landman, N.H., Schrag, D.P., 2013. The climate of the Late Cretaceous: New insights from the application of the carbonate clumped isotope thermometer to Western Interior Seaway macrofossil. Earth and Planetary Science Letters 362, 51–65.

Denton, E.J., Gilpin-Brown, J.B., 1966. On the buoyancy of the pearly *Nautilus*. Journal of the Marine Biological Association of the United Kingdom 46, 723–759.

Denton, E.J., Gilpin-Brown, J.B., 1973. Floatation mechanisms in modern and fossil cephalopods. Advances in Marine Biology 3, 197–268.

Dutta, A., Tekalur, S.A., Miklavcic, M., 2013. Optimal overlap length in staggered architecture composites under dynamic loading conditions. Journal of the Mechanics and Physics of Solids 61, 145–160.

Dzik, J., 1984. Phylogeny of the Nautiloidea. Palaeontologia Polonica 45, 3–203.

Dzik, J., Korn, D., 1992. Devonian ancestors of *Nautilus*. Palaontologische Zeitschrift 66, 81–98.

Erben, V.H.K., 1971. Anorganische und organische Schalenkomponenten bei *Cittarium pica* (L.) (Archaeogastropoda). Biomineralisation Forschungsberichte 3, 51–64.

Erben, V.H.K., 1972. Über die Bildung und das Wachstum von Perlmutt. Biomineralisation Forschungsberichte 4, 15–46.

Erben, H.K., Frajs, G., Siehl, A., 1969. Die Frohontogenetische Entwicklung der Schalenstruktur Ectocochileater Cephalopoden. Palaeontographica. Abt. A 132, 1–54.

Feng, Q.L., Su, X.W., Cui, F.Z., Li, H.D., 1995. Crystallographic orientation domains of flat

tablets in nacre. Biomimetics 3, 159–169.
Frýda, J., Bandel, K., Frýdová, B., 2009. Crystallographic texture of Late Triassic gastropod nacre: evidence of long-term stability of the mechanism controlling its formation. Bulletin of Geosciences 84, 745–754.
Frýda, J., Klicnarová, K., Frýdová, B., Mergl, M., 2010. Variability in the crystallographic texture of bivalve nacre. Bulletin of Geosciences 85, 645–662.
Frýda, J., Manda, Š., Rieder, M., Týcová, P., Haloda, J., Frýdová, B., Berkyová, S., Ferrová, L., 2008. Crystallographic textures of molluscan shells: a new tool unravelling their phylogeny. in: Budil, P. (Ed.), Palaeontological workshop held in honour of Doc. RNDr. Jaroslav Kraft, CSc.. Czech Geological Society, Prague, pp. 25–27.
Frýda,J., Weitschat, W., Tycova, P., Haloda, J., Mapes, R.H., 2007. Crystallographic textures of cephalopod nacre: its evolution, time stability, and phylogenetic significance. Seventh International Symposium, Cephalopods—Present and past, Sapporo Japan, Abstracts Volume, pp. 56–57
García-Ruiz, J.M., Checa, A., 1993. A model for the morphogenesis of ammonoid septal sutures. Geobios 26,157–162.
García-Ruiz, J.M., Checa, A., Rivas, P., 1990. On the origin of ammonite sutures. Paleobiology 16, 349–354.
Génio, L., Kiel, S., Cunha, M.R., Grahame, J., Little, C.T.S., 2012. Shell microstructures of mussels (Bivalvia: Mytilidae: Bathymodiolinae) from deep-sea chemosynthetic sites: Do they have a phylogenetic significance?. Deep Sea Research Part I: Oceanographic Research Papers 64, 86–103.
Gilbert, P.U.P.A., 2012. Polarization-dependent Imaging Contrast (PIC) mapping reveals nanocrystal orientation patterns in carbonate biominerals. Journal of Electron Spectroscopy and Related Phenomena 185, 395–405.
Gilbert, P.U.P.A., Metzler, R.A., Zhou, D., Scholl, A., Doran, A., Young, A., Kunz, M., Tamura, N., Coppersmith, S., 2008. Gradual ordering in red abalone nacre. Journal of the American Chemical Society 130, 17519–17527.
Grégoire C., 1962. On the submicroscopic structure of the *Nautilus* shell. Institut royal des Sciences naturelles de Belgique Bulletin 38, 1–71.
Grégoire C., 1987. Ultrastructure of the *Nautilus* shell. in: Saunders, W.B., Landman, N.H. (Eds.), *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York, 463–486.
Griesshaber, E., Schmahl, W.W., Ubhi, H.S., Huber, J., Nindiyasari, F., Maier, B., Ziegler, A., 2013. Homoepitaxial meso- and microscale crystal co-orientation and organic matrix network structure in *Mytilus edulis* nacre and calcite. Acta Biomaterialia 9, 9492–9502.

Gilpin-Brown, J.B., 1972. Buoyancy mechanisms of cephalopods in relation to pressure. Symposia of the Society for Experimental Biology 26, 251–259.

Hammer, Ø., 1999. The development of ammonite septa: an epithelial invagination process controlled by morphogens? Historical Biology 13, 153–171.

Hassan, M.A., Westermann, G.E.G., Hewitt, R.A., Dokainish, M.A., 2002. Finite-element analysis of simulated ammonoid septa (extinct Cephalopoda): septal and sutural complexities do not reduce strength. Paleobiology 28, 113–126.

House, M.R., 1987. Geographic distribution of *Nautilus* shells. in: Saunders, W.B., Landman, N.H. (Eds.), *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York, 53–64.

Hedegaard, C., Wenk, H.-R., 1998. Microstructure and texture patterns of mollusc shells. Journal of Molluscan Studies 64, 133–136.

Hewitt, R.A., Abdelsalam, U.A., Dokainish, M.A., Westermann, G.E.G., 1993. Comparison of the relative strength of siphuncles with prochoanitic and retrochoanitic septal necks by finite element analysis. in: House, M.R., (Ed.), The ammonoidea: environment, ecology, and evolutionary change. Academic Press, New York, 85–98.

Hewitt, R.A., Dokainish, M.A., El Aghoury, M., Westermann, G.E.G., 1989. Bathymetric limits of a Carboniferous orthoconic nautiloid deduced by finite element analysis. Palaios 4, 157–167.

Hewitt, R.A., Westermann, G.E.G., 1987. Nautilus Shell Architecture. in: Saunders, W.B., Landman, N.H. (Eds.), *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York, 435–461.

Hou, W.T., Feng, Q.L., 2003. Crystal orientation preference and formation mechanism of nacreous layer in mussel. Journal of Crystal Growth 258, 402–408.

Inoue, S., Kondo, S., 2016. Suture pattern formation in ammonties and the unknown rear mantle structure. Scientific Reports 6, 3689, 1–7.

Iwata, K., 1975. Ultrastructure of the conchiolin matrices in molluscan nacreous layer. Journal of the Faculty of Science, Hokkaido University. Series 4, Geology and Mineralogy 17, 173–229.

Jackson, D.J., MaDougall, C., Woodcroft, B., Moase, P., Rose, R.A., Kube, M., Reinhardt, R., Rokhsar, D.S., Montagnani, C., Joubert, C., Piquemal, D., Degnan, B.M., 2010. Parallel evolution of nacre building gene sets in molluscs. Molecular Biology and Evolution 27, 591–608.

Jäger, I., Fratzl, P., 2000. Mineralized collagen fibrils: A mechanical model with a staggered arrangement of mineral particles. Biophysical Journal 79, 1737–1746.

Kakisawa, H., Sumitomo, T., 2011. The toughening mechanism of nacre and structural materials

inspired by nacre. Science and Technology of Advanced Materials 12, 064710.
Kauffman, E.G., 1984. Paleobiogeography and evolutionary response dynamic in the Cretaceous Western Interior Seaway of North America. Geological Association of Canada Special Paper 27, 273–306.
Kauffman, E.G., Caldwell, W.G.E., 1993. The Western Interior Basin in space and time. Geological Association of Canada Special Paper 39, 1–30.
Keupp, H., Riedel, F., 1995. *Nautilus pompilius* in captivity: a case study of abnormal shell growth. Berliner geowissenschaftliche Abhandlungen Reihe E 16/2, 663–681.
Klug, C., Hoffmann, R., 2015. Ammonoid septa and suture. in: Klug, C., Korn, D., De Baets, K., Kruta, I., Mapes, R.H., (Eds.), Ammonoid Paleobiology: From anatomy to ecology, Springer, Dordrecht, pp. 45–90.
Klug, C., Kröger, B., Vinther, J., Fuchs, D., De Baets, K., 2015. Ancestry, origin and early evolution of ammonoids. in: Klug, C., Korn, D., De Baets, K., Kruta, I., Mapes, R.H., (Eds.), Ammonoid Paleobiology: From macroevolution to paleobiogeography, Springer, Dordrecht, pp. 3–24.
Klug, C., Meyer, E.P., Richter, U., Korn, D., 2008. Soft-tissue imprints in fossil and Recent cephalopod septa and septum formation. Lethaia 41, 477–492.
Kocks, U.F., Tomé, C.N., Wenk, H.-R., 1998. Texture and Anisotropy, Second Edition. Cambridge University Press, Cambridge.
Kröger, B., Vinther, J., Fuchs, D., 2011. Cephalopod origin and evolution: a congruent picture emerging from fossils, development and molecules. Bioessays 33, 602–613.
Kulicki, C., 1996. Ammonoid shell microstructure. in: Landman, N.H., Tanabe, K., Davis, R.A., (Eds.), Ammonoid Paleobiology, Springer, New York, pp. 65–101.
Kulicki, C., Tanabe, K., Landman, N.H., Kaim, A., 2015. Ammonoid shell microstructure. in: Klug, C., Korn, D., De Baets, K., Kruta, I., Mapes, R.H., (Eds.), Ammonoid Paleobiology: From macroevolution to paleobiogeography, Springer, Dordrecht, pp. 321–357.
Kummel, B. 1956. Post-Triassic nautiloid genera. Bulletin of the Museum of Comparative Zoology at Harvard College, 114, 321–494.
Kummel, B., 1964. Nautiloidea–Nautilida. in: Teichert, C., Kummel, B., Sweet, W.C., Stenzel, H.B., Furnish, W.M., Glenster, B.F., Erben, H.K., Moore, R.C., Zeller, D.E.N. (Eds.), Treatise on Invertebrate Paleontology, Part K, Mollusca 3. The University of Kansas Press, Lawrence, Kansas, pp. L383–L456.
Landman, N.H., Kennedy, W.J., Cobban, W.A., Larson, N.L., 2010. Scaphites of the "*Nodosus*" group from the Upper Cretaceous (Campanian) of the Western Interior of North America. Bulletin of the American Museum of Natural History Number 342, 1–242.
Lemanis, R., Korn, D., Zachow, S., Rybacki, E., Hoffmann, R., 2015. The evolution and

development of cephalopod chambers and their shape. PLoS ONE 11, e0151404.
Lemanis, R., Zachow, S., Hoffmann, R., 2016. Comparative cephalopod shell strength and the role of septum morphology on stress distribution. PeerJ 4, e2434.
Linzmeier, B.J., Kozdon, R., Peters, S.E., Valley, J.W., 2016. Oxygen isotope variability within *Nautilus* shell growth bands. PLoS ONE 11, e0153890.
MacClintock, C., 1967. Shell structure of patelloid and bellerophontoid gastropods (Mollusca). Peabody Museum of Natural History, Yale University, Bulletin 22, 1–140.
Machado, J., Lopes-Lima, M., Damasceno-Olivera, A., Colaço, A., Andrade, J., Silva, D., Jiménez-López, C., Rodríguez-Navarro, A., Checa, A., 2009. The influence of hydrostatic pressure on shell mineralization of *Anodonta cygnea*: A comparative study with a hydrothermal vent bivalve *Bathymodiolus azoricus*. Journal of Shellfish Research 28, 899–904.
Maier, B.J., Griesshaber, E., Alexa, P., Ziegler, A., Ubhi, H.S., Schmahl, W.W., 2014. Biological control of crystallographic architecture: Hierarchy and co-alignment parameters. Acta Biomaterialla 10 3866–3874.
Marler, R.T., Arora, J.S., 2004. Survey of multi-objective optimization methods for engineering. Structural and Multidisciplinary Optimization 26, 369–395.
Martin, A.W., Catala-Stucki, I., Ward, P.D., 1978, The growth rate and reproductive behavior of *Nautilus macromphalus*, Neues Jahrbuch für Geologie und Palaeontolgie Abhandlungen 156, 207–225.
Masuda, Y., Shinomiya, A., 1983. Genetic variation in *Nautilus pompilius*. Kagoshima University Research Center for South Pacific, Occasional Papers 1, 22–25.
Matsumoto, T., 1983. Cretaceous nautiloids from Hokkaido–I. Transactions and proceedings of the Paleontological Society of Japan. New Series 129, 9–25.
Meenakshi, V.R., Blackwelder, P.L., Wilbur, K.M., 1973. An ultrastructural study of shell regeneration in *Mytilus edulis* (Mollusca: Bivalvia). Journal of Zoology, London 171, 475–484.
Metzler, R.A., Abrecht, M., Olabisi, R.M., Ariosa, D., Johnson, C.J., Frazer, B.H., Coppersmith, S.N., Gilbert, P.U., 2007. Architecture of columnar nacre, and implications for its formation mechanism. Physical Review Letter 98, 268102.
Miall, A.D., Catuneanu, O., Vakarelov, B.K., Post, R., 2008. The Western Interior basin. in: Miall, A.D. (Ed.), The Sedimentary Basins of the United States and Canada. Elsevier, Amsterdam, 329–362.
Michibayashi, K., Mainprice, D., 2004. The role of pre-existing mechanical anisotropy on shear zone development within oceanic mantle Lithosphere: an example from the Oman ophiolite. Journal of Petrology 45, 405–414.

Miller, A.K., 1951. Tertiary Nautiloids of west-coastal Africa. Annales du Musée du Congo Belge. Série in 8°, Sciences géologiques 8, 1–88.

Miller, A.K., Furnish, W.M., Schindewolf, O.H., 1957. Paleozoic Ammonoidea. In: Arkell, W.J., Furnish, W.M., Kummel, B., Miller, A.K., Moore, R.C., Schindewolf, O.H., Sylvester-Bradley, P.C., Wright, W.C. (Eds.), Treatise on Invertebrate Paleontology, Part L, Mollusca 4. The University of Kansas Press, Lawrence, Kansas, pp. L11–L79.

Mitchell, P.R., Phakey, P.P., 1995. Notes on the microstructure of the *Nautilus* shell. Scanning Microscopy 9, 215–230.

Mukai, H., Saruwatari, K., Nagasawa, H., Kogure, T., 2010. Aragonite twinning in gastropod nacre. Journal of Crystal Growth 312, 3014–3019.

Mutvei, H., 1970. Ultrastructure of the mineral and organic components of molluscan nacreous layers. Biomineralisation Forschungsberichte 2, 48–72.

Mutvei, H., 1972a. Ultrastructural studies on cephalopod shells. Part I: The septa and siphonal tube in *Nautilus*. Bulletin of the Geological Institution of the University of Uppsala New Series 3, 237–261.

Mutvei, H., 1972b. Ultrastructural studies on cephalopod shells. Part II: Orthoconic cephalopods from the Pennsylvanian Buckhorn asphalt. Bulletin of the Geological Institution of the University of Uppsala New Series 3, 263–272.

Mutvei, H., 1972c. Ultrastructural relationships between the prismatic and nacreous layers in *Nautilus* (Cephalopoda). Biomineralisation Forschungsberichte 4, 80–86.

Mutvei, H., 1972d. Formation of nacreous and prismatic layers in *Mytilus edulis* L. (Lamellibranchiata). Biomineralisation Forschungsberichte 6, 96–100.

Mutvei, H., 1977. The nacreous layer in *Mytilus*, *Nucula*, and *Unio* (Bivalvia): Crystalline composition and nucleation of nacreous tablets. Calcified Tissue Research 24, 11–18.

Mutvei, H., 1983. Flexible nacre in the nautiloid *Isorthoceras*, with remarks on the evolution of cephalopod nacre. Lethaia 16, 233–240.

Mutvei, H., Dunca, E., 2008. Structural relationship between interlamellar organic sheets and nacreous tablets in gastropods and the cephalopod *Nautilus*. Paläontologische Zeitschrift 82, 85–94.

Mutvei, H., Dunca, E., 2010. Crystalline structure, orientation and nucleation of the nacreous tablets in the cephalopod *Nautilus*. Paläontologische Zeitschrift 84, 457–465.

Nishida, K., Ishimura, T., Suzuki, A., Sasaki, T., 2012. Seasonal changes in the shell microstructure of the bloody clam, *Scapharca broughtonii* (Mollusca: Bivalvia: Arcidae). Palaeogeography, Palaeoclimatology, Palaeoecology 363–364, 99–108.

Nishida, K., Suzuki, A., Isono, R., Hayashi, M., Watanabe, Y., Yamamoto, Y., Irie, T., Nojiri, Y., Mori, C., Sato, M., Sato, K., Sasaki, T., 2015. Thermal dependency of shell growth, microstructure, and stable isotopes in laboratory-reared *Scapharca broughtonii* (Mollusca: Bivalvia). Geochemistry, Geophysics, Geosystems 16, 2395–2408.

Nudelman, F., 2015. Nacre biomineralisation: A review on the mechanisms of crystal nucleation. Seminars in Cell & Developmental Biology 46, 2–10.

Nudelman, F., Gotliv, B.A., Addadi, L., Weiner, S., 2006. Mollusk shell formation: Mapping the distribution of organic matrix components underlying a single aragonitic tablet in nacre. Journal of Structural Biology 153, 176–187.

Oba, T., Kai, M., Tanabe, K., 1992. Early life history and habitat of *Nautilus pompilius* inferred from oxygen isotope examinations. Marine Biology 113, 211–217.

Olson, I.C., Gilbert, P.U.P.A., 2012. Aragonite crystal orientation in mollusk shell nacre may depend on temperature. The angle spread of crystalline aragonite tablets records the water temperature at which nacre was deposited by *Pinctada margaritifera*. Faraday Discussions 159, 421–432.

Olson, I.C., Kozdon, R., Valley, J.W., Gilbert, P.U.P.A., 2012. Mollusk shell nacre ultrastructure correlates with environmental temperature and pressure. Journal of the American Chemical Society 134, 7351–7358.

Olson, I.C., Blonsky, A.Z., Tamura, N., Kunz, M., Pokroy, B., Romao, C.P., White, M.A., Gilbert, P.U.P.A., 2013. Crystal nucleation and near-epitaxial growth in nacre. Journal of Structural Biology 184, 454–463.

Paganin, D., Mayo, S.C., Gureyev, T.E., Miller, P.R., Wilkins, S.W., 2002. Simultaneous phase and amplitude extraction from a single defocused image of a homogeneous object. Journal of Microscopy, 206, 33–40.

Pfaff, E., 1911. Uber Form und Bau der Ammonitensepten und ihre Beziehung zur Suturline. Jahreshefte des Niedersaechsischen Geologischen Vereins Hannover 4, 207–223.

Rabiei, R., Bekah, S., Barthelat, F., 2010. Failure mode transition in nacre and bone-like materials. Acta Biomaterialia 6, 4081–4089.

Rodriguez-Navarro, A.B., 2006. *XRD2DScan*: new software for polycrystalline materials characterization using two-dimensional X-ray diffraction. Journal of Applied Crystallography 39, 905–909.

Rodriguez-Navarro, A.B., 2007. Registering pole figures using an X-ray single-crystal diffractometer equipped with an area detector. Journal of Applied Crystallography 40, 631–634.

Rousseau, M., Lopez, E., Couté, A., Mascarel, G., Smith, D.C., Naslain, R., Bourrat, X., 2005a. Sheet nacre growth mechanism: a Voronoi model. Journal of Structural Biology 149, 149–157.

Rousseau, M., Lopez, E., Stempflé, P., Brendlé, M., Franke, L., Guette, A., Naslain, R., Bourrat, X., 2005b. Multiscale structure of sheet nacre. Biomaterials 26, 6254–6262.

Rousseau, M., Rollion-Bard, C., 2012. Influence of the depth on the shape and thickness of nacre tablets of *Pinctada margaritifera* pearl oyster, and on oxygen isotopic composition. Minerals 2, 55–64.

Saruwatari, K., Matsui, T., Mukai, H., Nagasawa, H., Kogure, T., 2009. Nucleation and growth of aragonite crystals at the growth front of nacres in pearl oyster, *Pinctada fucata*. Biomaterials 30, 3028–3034.

Sasaki, T., Shigeno, S., Tanabe, K., 2010. Anatomy of living *Nautilus*: Reevaluation of primitiveness and comparison with Coleoidea. in: Tanabe, K., Shigeta, Y., Sasaki, T. & Hirano, H. (Eds.), Cephalopods–Present and Past. Tokai University Press, Tokyo, pp.35–66.

Sato, K., Nakashima, R., Majima, R., Watanabe, H., Sasaki, T., 2013. Shell microstructures of five Recent solemyids from Japan (Mollusca: Bivalvia). Paleontological Research 17, 69–90.

Sato, K., Sasaki, T., 2015. Shell microstructure of Protobranchia (Mollusca: Bivalvia): Diversity, new microstructures and systematic implications. Malacologia 59, 45–103.

Saunders, W.B., 1984. The role and status of *Nautilus* in its natural habitat: Evidence from deep-water remote camera photosequences. Paleobiology 10, 496–486.

Saunders, W.B., 1987. The species of *Nautilus*. in: Saunders, W.B., Landman, N.H. (Eds.), *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York, 35–52.

Saunders, W.B., 1995. The ammonoid suture problem: relationships between shell and septum thickness and suture complexity in Paleozoic ammonoids. Paleobiology 21, 343–355.

Saunders, W.B., Ward, P.D., 1987. Ecology, distribution, and population characteristics of *Nautilus*. in: Saunders, W.B., Landman, N.H. (Eds.), *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York, 137–162.

Schäffer, T.E., Ionescu-Zanetti, C., Proksch, R., Fritz, M., Walters, D.A., Almqvist, N., Zaremba, C.M., Belcher, A.M., Smith, B.L., Stucky, G.D., Morse, D.E., Hansma, P.K., 1997. Does abalone nacre form by heteroepitaxial nucleation or by growth through mineral bridges? Chemistry of Materials 9, 1731–1740.

Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B., Tinevez, J.-Y., White, D.J., Hartenstein, V., Eliceiri, K., Tomancak, P., Cardona, A., 2012. Fiji: an open-source platform for biological-image analysis. Nature Methods 9, 676–682.

Schlögl, J., Chirat, R., Balter, V., Joachimski, M., Hudáčková, N., Quillévéré, F., 2011. *Aturia* from the Miocene Paratethys: An exceptional window on nautilid habitat and lifestyle, Palaeogeography, Palaeoclimatology, Palaeoecology 308, 330–338.

Schmidt, W.J., 1923. Bau und Bildung der Perlmuttermasse. Zoologische Jahrbücher Abteilung Anat Ontogenie Tiere 45, 1–148.

Schmidt, W.J., 1924. Die Bausteine des Tierkörpers in polarisiertem Licht. Friedrich Cohen, Bonn.

Seilacher, A., 1973. Fabricational noise in adaptive morphology. Systematic Zoology 22, 451–465.

Seilacher, A., 1975. Mechanische simulation und funktionelle evolution des Ammoniten-Septums. Paläontolische Zeischrift 49,268–286.

Sessa, J.A., Larina, E., Knoll, K., Garb, M., Cochran, J.K., Huber, B.T., MacLeod, K.G., Landman, N.H., 2015. Ammonite habitat revealed via isotopic composition and comparisons with co-occurring benthic and planktonic organisms. PNAS 112, 15562–15567.

Shigeta, Y., 1993. Post-hatching life history of Cretaceous Ammonoidea. Lethaia 26, 133–146.

Sinclair, B., Briskey, L., Aspden, W., 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.

Sinclair, W., Newman, S.J., Vianna, G.M.S., Williams, S., Aspden, W.J., 2011. Spatial subdivision and genetic diversity in populations on the East and West Coasts of Australia: The multi-faceted case of *Nautilus pompilius* (Mollusca, Cephalopoda). Reviews in Fisheries Science, 19, 52–61.

Sun, J., Bhushan, B., 2012. Hierarchical structure and mechanical properties of nacre: a review. RSC Advances 2, 7617–7632.

Takeda, Y., Tanabe, K., Sasaki, T., Landman, N.H., 2016. Durophagous predation on scaphitid ammonoids in the Late Cretaceous Western Interior Seaway of North America. Lethaia 49, 28–42.

Taylor, J.D., Kennedy, W.J., Hall, A., 1969. The shell structure and mineralogy of the Bivalvia. Introduction. Nuculacea–Trigonacea. Bulletin of the British Museum (Natural Hisotry) Zoology Supplement 3, 1–125.

Taylor, J.D., Kennedy, W.J., Hall, A., 1973. The shell structure and mineralogy of the Bivalvia II. Lucinacea–Clavagellacea conclusions. Bulletin of the British Museum (Natural Hisotry) Zoology 22, 255–294.

Taylor, J.D., Layman, M., 1972. The mechanical properties of bivalve (Mollusca) shell structures. Palaeontology 5, 73–87.

Taylor, B.E., Ward, P.D., 1983. Stable isotopic studies of *Nautilus macromphalus* Sowerby (New Caledonia) and *Nautilus pompilius* L. (Fiji). Palaeogeography, Palaeoclimatology, Palaeoecology 41, 1–16.

Teichert, C., 1964. Morphology of hard parts. in: Teichert, C., Kummel, B., Sweet, W.C., Stenzel, H.B., Furnish, W.M., Glenster, B.F., Erben, H.K., Moore, R.C., Zeller, D.E.N. (Eds.), Treatise on Invertebrate Paleontology, Part K, Mollusca 3. The University of Kansas Press, Lawrence, Kansas, pp. K13–K53.

Teichert C., Matsumoto, T., 1987. The ancestry of the genus *Nautilus*. in: Saunders, W.B., Landman, N.H. (Eds.), *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York, 25–32.

Trueman, A.E., 1940. The ammonite body-chamber, with special reference to the buoyancy and mode of Life of the living ammonite. Quarterly Journal of the Geological Society 96, 339–383.

Ubukata, T., 1994. Architectural constraints on the morphogenesis of prismatic structure in Bivalvia. Palaeontology 37, 241–261.

Uesugi, K., Hoshino, M., Yagi, N., 2011. Comparison of lens- and fiber-coupled CCD detectors for X-ray computed tomography. Journal of Synchrotron Radiation 18, 217–223.

Uesugi, K., Hoshino, M., Takeuchi, A., Suzuki, Y., Yagi, N., 2012. Development of fast and high throughput tomography using CMOS image detector at SPring-8. Proceedings of SPIE 8506, 85060I.

Uozumi, S., Suzuki, S., 1979. “Organic membrane-shell” and initial calcification in shell regeneration. Journal of the Faculty of Science, Hokkaido University. Series 4, Geology and mineralogy 19, 37–74.

Vandepas, L.E., Dooley, F.D., Barord, G.J., Swalla, B.J., Ward, P.D., 2016. A revisited phylogeography of *Nautilus pompilius*. Ecology and Evolution 6, 4924–4935.

Velázquez-Castillo, R.R., Reyes-Gasga, J., García-Gutierrez, D.I., Jose-Yacaman, M., 2006. Crystal structure characterization of nautilus shell at different length scales. Biomaterials 27, 4508–4517.

Vendrasco, M.J., Checa, A.G., Heimbrock, W.P., Baumann, S.D.J., 2013. Nacre in molluscs from the Ordovician of the Midwestern United States. Geosciences 3, 1–29.

Vendrasco, M.J., Checa, A.G., Kouchinsky, A.V., 2011. Shell microstructure of the early bivalve *Pojetaia* and the independent origin of nacre within the Mollusca. Palaeontology 54, 825–850.

Vendrasco, M.J., Rodríguez-Navarro, A.B., Checa, A.G., Devaere, L., Porter, S.M., 2015. To infer the early evolution of mollusc shell microstructures. Key Engineering Materials 672, 113–133.

Vincent, J.F.V., 1999. Determining the physical properties of skeletal materials. in: Savazzi., E., (Ed.), Functional Morphology of the Invertebrate Skeleton. John Wiley & Sons, West Sussex, England, 29–36.

Vincent, J.F.V., 2001. Ceramics from invertebrate animals. in: Levy, M., Bass, H.E., Stern, R.R., (Eds.), Handbook of elastic properties of solids, liquids, and gases vol. 3: Elastic properties of solids: Biological and organic materials, earth and marine sciences. Academic Press, San Diego, California, 213–226.

Wada, K., 1966. Spiral growth of nacre. Nature 211, 1427.

Wada, K., 1972. Nucleation and growth of aragonite crystals in the nacre of some bivalve molluscs. Biomineralisation Forschungsberichte 6, 141–159.

Ward, P.D., 1987. Natural history of *Nautilus.* Allen and Unwin, London.

Ward, P., Dooley, F., Barord, G.J., 2016a. *Nautilus*: biology, systematics, and paleobiology as viewed from 2015. Swiss Journal of Palaeontology 135, 169–185.

Ward, P.D., Flannery, D.T.O., Flannery, E.N., Flannery, T.F.F., 2016b. The Paleocene cephalopod fauna from Pebble Point, Victoria (Australia) – fulcrum between two Eras. Memoirs of Museum Victoria 74, 391–402.

Ward, P.D., Greenwald, L., Magnier, Y., 1981. The chamber formation cycle in *Nautilus macromphalus*. Paleobiology 7, 481–493.

Weiner, S., Traub, W., 1981. Organic-matrix-mineral relationships in mollusk-shell nacreous layers, in: Balaban, M., Sussman, J.L., Traub, W., Yonath, A. (Eds.), Structural Aspects of Recognition and Assembly in Biological Macromolecules. Balaban ISS, Rehovot and Philadelhia, pp. 467–482.

Wenk, H.-R., 1998. Typical textures in geological materials and ceramics. in: Kocks, U.F., Tomé, C.N., Wenk, H.-R. (Eds.), Texture and Anisotropy, Second Edition. Cambridge University Press, Cambridge, pp. 240–281.

Westermann, B., Beck-Schildwächter, I., Beuerlein, K., Kaleta, E.F., Schipp, R., 2004. Shell growth and chamber formation of aquarium-reared *Nautilus pompilius* (Mollusca, Cephalopoda) by X-Ray Analysis. Journal of Experimental Zoology 301A, 930–937.

Westermann, B., Schmidtberg, H., Beuerlein, K., 2005. Functional morphology of the mantle of *Nautilus pompilius* (Mollusca, Cephalopoda). Journal of Morphology 264, 277–285.

Wiedmann, J., 1960. Zur Systematik jungmesozoischer Nautiliden unter besonderer Berücksichtigung der iberischen Nautilinae d'Orb. Palaeontographica Abteilung A A115, 144–206.

Williams, R.C., Newman, S.J., Sinclair, W., 2012. DNA barcoding in *Nautilus pompilius* (Mollusca: Cephalopoda): evolutionary divergence of an ancient species in modern times. Invertebrate Systematics 26, 548–560.

Wise, S.W. Jr., 1970a. Microarchitecture and deposition of gastropod nacre. Science 167 1486–1488. Transactions of the American Microscopical Society 90, 376–380.

Wise, S.W., 1970b. Microarchitecture and mode of formation of nacre (Mother-of-Pearl) in

Pelecypods, Gastropods, and Cephalopods. Eclogae Geologicae Helvetiae 63, 775–797.

Wray, C.G., Landman, N.H., Saunders, W.B., Bonacum, J., 1995. Genetic divergence and geographic diversification in *Nautilus*. Paleobiology 21, 220–228.

Wright, C.W., Calloman, J.H., Donovan, D.T., Howarth, M.K., 1996. Cretaceous Ammonoidea. Treatise on Invertebrate Paleontology, Part L, Mollusca 4 (Revised) 4, 1–362.

Yang, W., Kashani, N., Li, X.-W., Zhang, G.-P., Meyers, M.A., 2011b. Structural characterization and mechanical behavior of a bivalve shell (*Saxidomus purpuratus*). Materials Science and Engineering C 31, 724–729.

Yang, W., Zhang, G.P., Zhu, X.F., Li, X.W., Mayers, M.A., 2011a. Structure and mechanical properties of *Saxidomus purpuratus* biological shells. Journal of the Mechanical Behavior of Biomedical Materials 4, 1514–1530.

Yao, N., Epstein, A., Akey, A., 2006. Crystal growth via spiral motion in abalone shell nacre. Journal of Materials Research 21, 1939–1946.

Yao, N., Epstein, A.K., Liu, W., Sauer, F., Yang, N., 2009. Organic–inorganic interfaces and spiral growth in nacre. Journal of the Royal Society Interface 6, 367–376.

Zakharov, Y.D., Shigeta, Y., Nagendra, R., Safronov, P.P., Smyshlyaeva, O.P., Popov, A.M., Velivetskaya, T.A., Afanasyeva, T.B., 2011. Cretaceous climate oscillations in the southern palaeolatitudes: New stable isotope evidence from India and Madagascar. Cretaceous Research 32, 623–645.

Zakharov, Y.D., Tanabe, K., Shigeta, Y., Safronov, P.P., Smyshlyaeva, O.P., Dril, S.I., 2016. Early Albian marine environments in Madagascar: An integrated approach based on oxygen, carbon and strontium isotopic data. Cretaceous Research 58, 29–41.

Appendix Table

5 年以内に雑誌などで刊行予定のため、非公開。