Pearl formation in an Early Cretaceous belemnite

Kevin Stevens¹ · René Hoffmann¹ · Marie-Claire Picollier² · Jörg Mutterlose¹

Received: 23 January 2020 / Accepted: 30 April 2020 / Published online: 25 May 2020
© The Author(s) 2020

Abstract

Many aspects of the paleobiology and biomineralization of belemnites, the most common fossil coleoid cephalopods of the Mesozoic, are still unclear. Here, we describe a pearl from an Early Cretaceous belemnite rostrum (*Duvalia emerici*) using high-resolution micro-CT imaging. After initial formation of a free pearl within the soft tissue, the pearl was fused to the rostrum and later overgrown by rostrum increments, thereby forming a blister pearl. The contact zone of the pearl with the rostrum shows resorption and deformation of earlier rostrum increments. Formation of a free pearl inside the soft tissue of the belemnite demonstrates a relatively thick (min. 5.6 mm) tissue layer surrounding the rostrum in this species. Our data show that classification of paleopathologies based on external features alone might lead to false inferences of formation mechanisms.

Keywords Belemnite · Pearl · Paleopathology · Micro-CT · Cretaceous · Biomineralization

Introduction

Contrary to common belief, natural true pearls do not form due to the entrapment and subsequent enclosure of sediment particles, parasites, or other irritants by biominerals (usually nacre), but are the result of the displacement of mantle epithelium cells into the mantle tissue due to tissue damage. These displaced mantle epithelium cells form a so-called pearl sac inside the tissue in which the pearl then forms. Tissue damage might be caused by predators or parasites inside the mantle tissue (Alverdes 1920; Taylor and Strack 2008; Hänni 2012). Pearls that after their free growth connect with the shell and attach to it are called blister pearls, while blisters are any protuberance that encapsulates foreign

material or parasites (Taylor and Strack 2008). Pearl and blister formations are common in bivalves and gastropods, and blisters have been described for ammonites and belemnites (e.g., Mietchen et al. 2005; De Baets et al. 2011, 2015; Keupp 2012; Hoffmann et al. 2014, 2018a, 2020). A parasite-induced blister on a belemnite rostrum has recently been described in detail by Hoffmann et al. (2018a). True pearls are unknown from modern coleoids, only a blister has been reported by Keupp (2012) and Hoffmann et al. (2018b) for *Spirula spirula*. Spherical structures attached to the cuttlebone chambers of *Sepia officinalis* (Gutowska et al. 2010) are unlikely to represent true pearls as they formed synchronously with the chambers.

Blisters usually cannot be differentiated from true blister pearls by the surface of a specimen only. Their differentiation requires invasive or non-invasive methods such as sectioning, grinding, or computed tomography to reveal internal structures (e.g., De Baets et al. 2011; Hoffmann et al. 2014, 2020). However, distinction between blisters and blister pearls is important due to their different origins and formation modes.

Belemnites were common, superficially squid-like, Mesozoic coleoid cephalopods, whose calcitic rostra are frequently used as geochemical archives (e.g., Urey et al. 1951; Veizer et al. 1999; Mutterlose et al. 2010; Ullmann et al. 2014). The biomineralization process of belemnites is

Handling editor: Christian Klug.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s12542-020-00521-y>) contains supplementary material, which is available to authorized users.

✉ Kevin Stevens
kevin.stevens@rub.de

¹ Institut für Geologie, Mineralogie und Geophysik, Ruhr-Universität Bochum, Universitätsstr. 150, 44801 Bochum, Germany

² La Vionie, 24160 Saint-Pantalay-d'Excideuil, France

still under discussion, because there is no modern equivalent of a calcitic internal shell structure in today's coleoid cephalopods (Hoffmann et al. 2016; Stevens et al. 2017; Hoffmann and Stevens 2020).

We present high-resolution micro-CT data of a pathological belemnite rostrum (*Duvalia emerici*) with a blister pearl, reconstruct its formation, and discuss implications for belemnite paleobiology, biomineralization, and the interpretation of pathological rostra in general.

Materials and methods

The studied specimen [*Duvalia emerici* (Raspail, 1829)] comes from the upper Valanginian (*Saynoceras verrucosum* Zone) of the La Palud section in the village of Aulan, south-eastern France, about 100 km north of Marseille (Fig. 1). The La Palud section exposes fossiliferous hemipelagic calcareous mudstones of Valanginian to earliest Hauterivian age, which yield diverse belemnites of the genera *Castellanibelus*, *Conobelus*, *Duvalia*, *Pseudobelus*, and *Hibolithes*. *Duvalia emerici* represents the most common belemnite of the *S. verrucosum* Zone at La Palud. An overview of duvaliid belemnites from the Lower Cretaceous of France is given by Combémourel (1973). The La Palud section is at present

not accessible, but the section is lithologically, stratigraphically, and paleontologically comparable to the close-by Barret-le-Bas section (Busnardo et al. 1979). The studied specimen is kept in the collection of the Ruhr-Universität Bochum (RUB-Pal 39073). The rostrum has a total length (*L*) of 66.4 mm, height (*Dv*) of 28.5 mm, and width (*DI*) of 15.1 mm at the protoconch level.

Microtomographic data of the *D. emerici* rostrum were collected with the nanotom m device of the iWP company (Neuss, Germany). The first scan was conducted with 105 keV X-ray and has a resolution of 31- μ m isotropic voxel size for the whole rostrum resulting in a volume file of 2.98 gigabytes with 1034 $\times$ 617 $\times$ 2398 slides in *x*-, *y*-, and *z*-direction. This scan has been used to extract surface images of the rostrum (Fig. 2). The second scan is a close-up of the pearl with a 105 keV X-ray beam, with a resolution of 12.9 μ m isotropic voxel size resulting in a volume file of 16.4 gigabytes with 2384 $\times$ 1651 $\times$ 2139 slides in *x*-, *y*-, and *z*-direction (Fig. 3). The specimen was imaged with a DXR-500L 3072 $\times$ 2400-pixel detector with 500 ms exposure time for both scans. Due to the large file size, CT data are archived at the Ruhr-Universität Bochum. Original CT data will be made available by the authors at individual request.

Results

The studied rostrum shows a hemispherical structure on its left ventrolateral side (Fig. 2). Growth increments and growth stages in this specimen can be discerned by CT scanning due to different amounts of organics occluded within the calcite (Hoffmann et al. 2020). The CT data revealed that this hemispherical structure is the surface expression of growth increments covering a sphere with a diameter of 5.6 mm. This sphere is composed of concentric calcite layers and is attached to the rostrum. The layers of the rostrum in direct contact with this sphere were partly resorbed and deformed and the sphere overgrown by rostrum increments formed later (Fig. 3, Supplementary Material).

Interpretation and discussion

Micro-CT imaging of belemnite rostra is a powerful, non-invasive method for the investigation of their internal structure (Hoffmann et al. 2018a, 2020). The present study demonstrates this further by showing that ontogenetic growth surfaces of belemnite rostra are discernible via CT, allowing for the reconstruction of growth stages. The following stages of blister pearl formation in our *Duvalia emerici* are suggested: (1) damage to the mantle epithelium results in

Fig. 1 Location of the village of Aulan in south-eastern France. Map compiled with generic mapping tools (Wessel et al. 2019)

Fig. 2 **a–d** CT surface rendering of the *Duvalia emerici* specimen. **a** left lateral view, **b** ventral view, **c** right lateral view, **d** dorsal view. **e–g** Photographs of the specimen from inclined dorsal view to lateral view. Scale bar is 1 cm

formation of a pearl sac, (2) formation and growth of a free pearl inside the pearl sac, (3) contact between the rostrum surface and the free pearl, (4) resorption and deformation of rostrum increments in contact with the pearl, and (5) overgrowth of the pearl with rostrum increments (Figs. 3, 4). This formation model characterizes the structure as a true blister pearl, that is, a pearl that after its initial formation inside the mantle tissue became attached to the mineralized shell, in our case, the rostrum (cf. Taylor and Strack 2008). Fusion of the free pearl with the rostrum after its initial formation is responsible for its preservation. Non-blister pearls of belemnites can be considered to have been usually lost after decomposition of the belemnite soft tissue.

The thickness of the tissue that covered belemnite rostra is largely unknown (Hoffmann and Stevens 2020). The maximum diameter of the free pearl (5.6 mm) can be interpreted as giving the minimum mantle tissue thickness of *D. emerici*, because pearls form completely embedded inside the mantle tissue in modern mollusks (e.g., Taylor and Strack 2008). This argues for a relatively thick (min. 5.6 mm) tissue in this species and probably against suggestions of extremely thin or no tissue covering of belemnite rostra based on supposedly *syn vivo* barnacle borings and rostrum color patterns (e.g., Seilacher 1968; Jordan et al. 1975; Seilacher and Gishlick 2015).

CT scanning of belemnite rostra demonstrates that externally similar-looking pathologies might have different causes. A similar but less well-developed protuberance in a *D. emerici* rostrum was recently described by Hoffmann et al. (2020), which CT scanning revealed to be a blister and not a blister pearl. Based on studies of pathological ammonites by Hölder (1956), Keupp (2012) extended Hölder's classification of pathologies as so-called forma aegra types to coleoids. Under this scheme, the here described pathology would be categorized as the forma aegra *bullata*, which following Keupp (2012) comprises blisters due to parasite infection or incorporation of other foreign material. However, its internal structure of concentric layers forming a sphere clearly indicates that the structure described here is a blister pearl and not a blister. The descriptive term forma aegra *bullata* does not account for internal features only made visible via sectioning or scanning. Potential pearl formations in belemnites were summarized under forma aegra *granulata* by Keupp (2012). This phenotype, however, clearly differs from the blister pearl by being characterized by a coarsely granulated rostrum surface. While the *Hibolites* specimen pictured by Keupp (2012, Fig. 384) as an example for forma aegra *granulata* might display true pearls, the specimen figured by Radwańska and Radwański

Fig. 3 a–p Individual fly-through images of the blister pearl from dorsal to ventral. **q** Close-up of the blister pearl. The spherical shape of the free pearl (border = stippled line) made up of concentric layers is clearly visible as well the resorption and deformation surfaces of earlier rostrum increments (fine stippled line) and later overgrowth of the free pearl. Further visible features are pyrite and organic-rich areas. The diffuse white area at the outer border of the blister pearl is a beam hardening artefact. A fly-through video is available as Supplementary Material. Scale bar is 0.5 cm

(2004) and cited by Keupp (2012) represents an example of a restart point of rostrum fiber nucleation, caused by cessation of syntaxial growth of rostrum fibers and new fiber nucleation (Stevens et al. 2017). The utility of forma aegra types to describe and infer formation mechanisms from pearls and related structures is therefore limited. For pearls and similar structures, the established descriptive terms blister, (free) pearl, and blister pearl should be preferred instead (cf. Taylor and Strack 2008). Structures externally similar to the one described herein, in which imaging of internal structures is not possible due to preservation should be termed protuberance or might be referred to the forma aegra *bullata*. However, usage of forma aegra *bullata* should not imply a certain internal structure or formation process. Using the straightforward term protuberance circumvents implying a specific formation mechanism and should therefore be preferred. Forma aegra types are still useful for specific arrangements of protuberances, for example, coarsely granulated surfaces (forma aegra *granulata*).

Conclusions

The herein described hemispherical protuberance on an Early Cretaceous *Duvalia emerici* belemnite rostrum represents a true blister pearl, i.e., a pearl that was fused to the rostrum surface after its initial formation inside the mantle tissue as a free pearl. The contact zone of the pearl with the rostrum shows resorption and deformation of earlier rostrum increments. To form this free pearl, the rostrum in this species must have been covered in at least 5.6 mm thick tissue, arguing against claims of extremely thin or no tissue covering of belemnite rostra. The internal structure of the blister pearl illustrates that paleopathologies should not be classified and interpreted based on external features alone, as this might lead to false inferences of formation mechanisms.

Fig. 4 Formation model of the blister pearl displayed with a schematic cross section. **a** Damage to the tissue results in formation of a pearl sac of displaced mantle epithelium cells, **b** a pearl (dark gray) forms inside the pearl sac, **c** the pearl grows and comes into contact with the rostrum (medium gray) surface, **d** rostrum increments in contact with the pearl are resorbed and deformed, **e** the pearl is overgrown by rostrum increments, forming a blister pearl

Acknowledgements Open Access funding provided by Projekt DEAL. We thank Hendrik Wesendonk of iWP for assistance with the CT scans. We are further thankful to reviewers Benjamin Linzmeier and Kenneth de Baets as well as editors Mike Reich and Christian Klug whose comments and suggestions significantly improved this contribution.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Alverdes, F. 1920. Über Perlen und Perlenbildung. *Naturwissenschaftliche Wochenschrift (Neue Folge)* 19: 481–484.
- Busnardo, R., J.P. Thieuloy, and M. Moullade. 1979. Hypostratotype mesogéenne de l'étage Valanginien (sud-est de la France). *Éditions du CNRS Vol. 6: Les stratotypes français*, 1–143.
- Campana, S.E., and J.D. Neilson. 1985. Microstructure of Fish Otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1014–1032. <https://doi.org/10.1139/f85-127>.
- Combémourel, R. 1973. Les Duvaliidae (Pavlow) du crétacé inférieur français. *Document des laboratoires de géologie de la faculté des sciences de Lyon* 57: 131–186.
- De Baets, K., C. Klug, and D. Korn. 2011. Devonian pearls and ammonoid-endoparasite co-evolution. *Acta Palaeontologica Polonica* 56: 159–180.
- De Baets, K., H. Keupp, and C. Klug. 2015. Parasites of ammonoids. In *Ammonoid paleobiology: From anatomy to ecology*, eds. C. Klug, D. Korn, K. De Baets, I. Kruta, and R.H. Mapes, 837–875. Dordrecht: Springer Netherlands.
- Gutowska, M.A., F. Melzner, H.O. Pörtner, and S. Meier. 2010. Cuttlebone calcification increases during exposure to elevated seawater pCO₂ in the cephalopod *Sepia officinalis*. *Marine Biology* 157: 1653–1663. <https://doi.org/10.1007/s00227-010-1438-0>.
- Hänni, H.A. 2012. Natural pearls and cultured pearls: A basic concept and its variations. *The Australian Gemmologist* 24: 9.
- Hoffmann, R., and K. Stevens. 2020. The palaeobiology of belemnites—Foundation for the interpretation of rostrum geochemistry. *Biological Reviews* 95: 94–123.
- Hoffmann, R., J.A. Schultz, R. Schellhorn, E. Rybacki, H. Keupp, S.R. Gerden, R.E. Lemanis, and S. Zachow. 2014. Non-invasive imaging methods applied to neo- and paleo-ontological cephalopod research. *Biogeosciences* 11: 2721–2739. <https://doi.org/10.5194/bg-11-2721-2014>.
- Hoffmann, R., D.K. Richter, R.D. Neuser, N. Jöns, B.J. Linzmeier, R.E. Lemanis, F. Füsseis, X. Xiao, and A. Immenhauser. 2016. Evidence for a composite organic–inorganic fabric of belemnite rostra: Implications for palaeoceanography and palaeoecology. *Sedimentary Geology* 341: 203–215. <https://doi.org/10.1016/j.sedgeo.2016.06.001>.
- Hoffmann, R., J. Ansorge, H. Wesendonk, and K. Stevens. 2018a. A Late Cretaceous pathological belemnite rostrum with evidence of infection by an endoparasite. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 287: 335–349. <https://doi.org/10.1127/njgpa/2018/0720>.
- Hoffmann, R., R.E. Lemanis, L. Wulff, S. Zachow, A. Lukeneder, C. Klug, and H. Keupp. 2018b. Traumatic events in the life of the deep-sea cephalopod mollusc, the coleoid *Spirula spirula*. *Deep Sea Research Part I: Oceanographic Research Papers* 142: 127–144.
- Hoffmann, R., K. Stevens, M.-C. Picollier, J. Mutterlose, and C. Klug. 2020. Non-destructive analysis of pathological belemnite rostra by micro-CT techniques. *Acta Palaeontologica Polonica* 65: 11–27. <https://doi.org/10.4202/app.00689.2019>.
- Hölder, H. 1956. Über Anomalien an jurassischen Ammoniten. *Paläontologische Zeitschrift* 30: 95–107.
- Jordan, R., L. Scheuermann, and C. Spaeth. 1975. Farbmuster auf jurassischen Belemniten-Rostren. *Paläontologische Zeitschrift* 49: 332–343.
- Keupp, H. 2012. Atlas zur Paläopathologie der Cephalopoden. *Berliner paläobiologische Abhandlungen* 12: 1–392.
- Mietchen, D., H. Keupp, B. Manz, and F. Volke. 2005. Non-invasive diagnostics in fossils—Magnetic resonance imaging of pathological belemnites. *Biogeosciences* 2: 133–140. <https://doi.org/10.5194/bg-2-133-2005>.
- Mutterlose, J., M. Malkoc, S. Schouten, J.S. Sinninghe Damsté, and A. Forster. 2010. TEX₈₆ and stable δ¹⁸O paleothermometry of early Cretaceous sediments: Implications for belemnite ecology and paleotemperature proxy application. *Earth and Planetary Science Letters* 298: 286–298. <https://doi.org/10.1016/j.epsl.2010.07.043>.
- Radwańska, U., and A. Radwański. 2004. Disease and trauma in Jurassic invertebrate animals of Poland: An updated review. *Volumina Jurassica* 2: 99–112.
- Raspail, F.-V. 1829. Histoire naturelle des Bélemnites, accompagnée de la description et de la classification des espèces. *Annales scientifiques d'observation I*: 271–331.
- Seilacher, A. 1968. Swimming habits of belemnites—recorded by boring barnacles. *Palaeogeography, Palaeoclimatology, Palaeoecology* 4: 279–285.
- Seilacher, A., and A.D. Gishlick. 2015. *Morphodynamics*. Boca Raton: CRC Press.
- Stevens, K., E. Griesshaber, W. Schmahl, L.A. Casella, Y. Iba, and J. Mutterlose. 2017. Belemnite biomineralization, development, and geochemistry: The complex rostrum of *Neohibolites minimus*. *Palaeogeography, Palaeoclimatology, Palaeoecology* 468: 388–402.
- Taylor, J., and E. Strack. 2008. Pearl production. In *The pearl oyster*, eds. P.C. Southgate and J.S. Lucas, 273–302. Amsterdam: Elsevier. <https://doi.org/10.1016/B978-0-444-52976-3.00008-5>.
- Ullmann, C.V., N. Thibault, M. Ruhl, S.P. Hesselbo, and C. Korte. 2014. Effect of a Jurassic oceanic anoxic event on belemnite ecology and evolution. *Proceedings of the National Academy of Sciences* 111: 10073–10076.
- Urey, H.C., H.A. Lowenstam, S. Epstein, and C.R. McKinney. 1951. Measurement of paleotemperature and temperature of the Upper Cretaceous of England, Denmark and the southern United States. *Bulletins of the Geological Society of America* 62: 399–416.
- Veizer, J., D. Ala, K. Azmy, P. Bruckschen, D. Buhl, F. Bruhn, G.A.F. Carden, A. Diener, S. Ebner, Y. Godderis, T. Jasper, C. Korte, F. Pawellek, O.G. Podlaha, and H. Strauss. 1999. ⁸⁷Sr/⁸⁶Sr, δ¹³C and δ¹⁸O evolution of Phanerozoic seawater. *Chemical Geology* 161: 59–88.
- Wessel, P., J.F. Luis, L. Uieda, R. Scharroo, F. Wobbe, W.H.F. Smith, and D. Tian. 2019. The generic mapping tools version 6. *Geochemistry, Geophysics, Geosystems*. <https://doi.org/10.1029/2019GC008515>.