Exceptional preservation of the endolithic trace fossil
*Dendrina belemnitica* Mägdefrau, 1937

in the Upper Maastrichtian greensand of Nasiłów (central Poland)

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**KEYWORDS** - *Dendrina*, Bioerosion, Borings, Preservation, Chalk, Glauconitic Sand.

**ABSTRACT** - The rosette-shaped endolithic trace fossil *Dendrina belemnitica* Mägdefrau, 1937 is common in biogenic substrates in the Upper Cretaceous facies of Europe but badly preserved. Chalk specimens are affected by an intensive calcite cementation. Basically all parts of borings are secondarily sealed if their internal diameter is less than the size of the cement crystals and application of casting-embedding techniques fails to document the morphology of such borings. Therefore, up to now only the macro-morphology of *Dendrina*-borings could be detected in specimens of the chalk facies.

In contrast, biogenic calcitic substrates found in the Upper Maastrichtian greensand of Nasiłów in central Poland remained almost unaltered diagenetically. In these specimens calcite cementation did not occur and endolithic traces can be studied at an exceptional high-resolution. Accordingly, new morphological features of the ichnospecies *D. belemnitica* can be described. Casts of the *Dendrina*-boring systems show a cover of unbranched hair-like extensions. Those extensions spread into the substrate from all surfaces of the boring and give the *Dendrina*-casts a hairy or furry appearance. Most likely they had an exploratory function in limited substrates, i.e. locating the boundaries of the substrate and investigating cavities within it. The proof of hair-like extensions that could have enabled sensory functions can explain the stenomorphic reactions of the *Dendrina*-producer for the first time. Some casts of the hair-like extensions exhibit bulbous swellings. Most probably these structures represent the second phase of the boring process, followed by further expansion and fusion that constitute the typically verrucose *Dendrina*-rosette. The endolithic trace *D. belemnitica* can functionally be compared with a foraminiferan test, and a test-less foraminiferan species is considered to be the trace-making organism.

**INTRODUCTION**

The rosette-shaped boring *D. belemnitica* is conspicuous in the translucent calcite rostra of European Upper Cretaceous belemnites. Already by the 19th century endolithic trace fossils had attracted the attention of scientists, such as Friedrich von Hagenow (1797-1865) and Friedrich August von Quenstedt (1809-1889). However, their early descriptions based on externally visible features are insufficient (Hagenow, 1840, p. 670; Quenstedt, 1849, p. 470-471). Significant features of sub-millimetric scale, like the apertures on the substrate surface connecting the lumen of the endolithic system with the exterior, remained undiscovered. Without this evidence, discussing the probability of a parasitic origin of *D. belemnitica* was difficult (Quenstedt, 1849, p. 470-471).

A new impetus to ichnological research was given by the introduction of the cast-embedding technique coupled with scanning electron microscopy. The two methods enabled the detection of hitherto hidden structures of endolithic traces. However, these methods are limited in substrates from carbonate depositional environments that are commonly affected by heavy cementation (Schnick, 1999). For instance there are no xenoglyphs preserved on the internal surfaces of such specimens (Bromley & D’Alessandro, 1984, p. 237). Neither the texture of the host substrate nor the original surface morphology of the boring are visible as they are curved by a diagenetic calcite cement layer. In addition, there may be a fill of fine sediment particles (coccoliths, etc.) inside the boring that also deteriorates the quality of the cast. The surface of the resin casts always appears spongiform and the mostly...
thin voids of the boring system are completely sealed by calcite cement. Therefore, an artificial resin cast cannot display the comprehensive morphology of chalk specimen of *D. belemniticola*.

The obviously stenomorphic boring behavior of the *Dendrina*-producer can be understood as indirect evidence of incomplete preservation. Doubtless it must have had the ability to avoid contact with either the outer substrate surface or other endolithic traces. This provoked a search for better-preserved *Dendrina* specimens. After examining several hundred Upper Cretaceous belemnite rostra from North Germany, Denmark and Poland, diagenetically almost unaltered belemnite rostra were discovered in the Upper Maastrichtian Nasiłów greensand. Further investigations have focused on these excellently preserved specimens.

**LOCALITY**

Nasiłów is located in the central Polish Middle Vistula Valley (Fig. 1). Throughout the Late Cretaceous the study area was part of the Danish-Polish Trough, which extends southeastwardly to the Lviv region in western Ukraine. The investigated greensand deposits terminate the Upper Cretaceous sequence of siliceous limestones (“opokas”) exposed along the Middle Vistula Valley, between Annopol-on-Vistula and Puławy. The greensand covers an uppermost Maastrichtian hardground (Fig. 1c), and is overlain by the post-Cretaceous so called “Siwak-series” (Blaszkiewicz, 1980; Abdel-Gawad, 1986; Machalski & Walaszczyk, 1987; 1996; Walaszczyk et al., 1999).

Machalski & Walaszczyk (1987) have recognized unphosphatized Maastrichtian, phosphatized Maastrichtian and Danian fossil assemblages in the Nasiłów greensand. Their co-existence is based on condensation and mixing processes resulting in the formation of a residual lag.

**MATERIAL AND METHODS**

The material investigated belongs to the unphosphatated Maastrichtian assemblage. Beside the *Dendrina*-bearing cephalopods *Belemnella kazimiroviensis* (Skolozdrowna, 1932) and *B. pensaensis* (Najdin, 1952), the assemblage comprises also fossil sponges, serpulids, brachiopods, bivalves and echinoids (Machalski & Walaszczyk, 1987, tab. 2). The calcite of the rostra is translucent and endolithic traces are clearly visible, both in transmitted and reflected light microscopy. Diagenetic calcite cementation is lacking.

Endolithic traces in more than 120 belemnites and belemnite fragments as well as calcitic bivalve and brachiopod shells were initially examined. Those containing *D. belemniticola* were assessed microscopically and selected for further preparation according to the cast-embedding technique (Golubic et al., 1970, 1983) in the Geological-Palaeontological Institute of Frankfurt am Main University in 1990. Prior to the embedding in epoxy resin Araldite (Fluka Chemie AG Buchs, Switzerland) the specimens were treated using...
specimens were selected has, stenomorphically modified -rosettes always fit isp. and isp. (Figs 2, 3c).

Entobia appear indistinct in contrast to those of Dendrina belemniticola Mägdefrau, 1937, Hyellomorpha microdendritica Vogel, Golubic & Brett, 1987, Entobia isp. and Trypanites isp. (Figs 2, 3c). A xenomorphic overprint of preexisting traces has not yet been observed.

In addition to observations concerning the boring behavior of the trace maker, a remarkable detail concerning the microstructure of D. belemniticola has been observed in the Nasiłów material. The contours of D. belemniticola appear indistinct in contrast to those of other endolithic traces (Fig. 3c).

Scanning electron microscopy (SEM) - morphological details

SEM investigations became necessary to verify the assumptions concerning the behavior of the trace maker indicated by reflected light microscopy. Applying SEM techniques, complex microstructures were observed covering several orders of magnitude. The largest refers to morphological details with dimensions of a few µm. Smaller order structures occur at a tenfold smaller scale. During the examination of casts, covers of unbranched, hair-like extensions were detected. These spread into the substrate from all parts of the boring, except the initial penetration tunnel, and give the Dendrina-casts a hairy or furry appearance (Figs 3c-d, 4). Some of the hair-like extensions exhibit swellings in the dimension of the verrucose surface morphology of the rosette (Fig. 5d, f). Most probably these structures represent the successive boring process: proximal parts of the hair-like extensions expand to bulbous swellings that unify and form finally the verrucose surface of the Dendrina-rosette.

RESULTS

Observations in reflected light - macro morphology

The undisturbed-idiomorphic formation of the Dendrina-boring system starts with an isodiametric tunnel that penetrates into the substrate to the depth necessary for the rosette to be bored. The tunnel expands laterally ("balloon-stage"). From these expansions lobes spread close to the substrate surface, almost touching it. Initially, the young rosette grows into a more or less bilateral butterfly-like shape ("butterfly-stage"). Subsequently, this early pattern is overprinted by further branching, lateral growth and anastomosis of adjacent lobes. The mature Dendrina-system is nearly circular in shape but irregularly subdivided by a few narrow substrate septa between the lobes of the rosette (Figs 2-4).

In addition to idiomorphically developed Dendrina-rosettes, there are also stenomorphically modified specimens. Their growth pattern is adapted to the surface morphology of the substrate or preexisting endolithic voids. For example, the Dendrina-rosettes always fit the curved surface of belemnite rostra. The smaller the diameter of the rostrum, the greater is the bending of the endolithic rosette, maintaining an equal distance between rosette and substrate surface. Dendrina-rosettes show a comparable pattern beneath unevenly fractured surfaces of belemnites and corrugated shells of pectinid bivalves. In the latter case the traces follow the corrugations of the substrate to prevent any contact with the outer shell surface.

A more pronounced type of stenomorphism is caused by preexisting or synchronously developed voids (Figs 2, 3a-c). Any contact or even the amalgamation with these voids is prevented. In the case of convergent growth of two Dendrina-rosettes, both are possible: the lateral interlocking of rosette lobes in the same tier as well as the formation of rosette piles (Figs 2, 3b, 7b). This behavior is also found at the potential contact with other endolithic traces, such as Dendrina anomala Mägdefrau, 1937, Hyellomorpha microdendritica Vogel, Golubic & Brett, 1987, Entobia isp. and Trypanites isp. (Figs 2, 3c). A xenomorphic overprint of preexisting traces has not yet been observed.

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an ultrasonic cleaner. After curing, the resin blocks were cut and decalcified in dilute hydrochloric acid (5%). The casts, now showing the positive infills of the borings, were rinsed with distilled water, dried in a critical point dryer Pelco CPD2 (Ted Pella Inc., U.S.A.), mounted, and sputter-coated with gold for investigation by scanning electron microscopy. The SEM investigations were carried out using a BS 350 SEM (Tesla Brno, Czech Republic former CSSR) in the Biological Institute of Greifswald University in 1991.

Other D. belemniticola specimens were selected for thin section preparation. The rosette-bearing parts of the belemnite rostra were sectioned transversally. Examination of the thin sections was undertaken using transmitted-light microscopy (Zeiss Axioskope 50 and Zeiss AxioCam HRo, Carl Zeiss Microscopy GmbH Göttingen, Germany).

The investigated material is part of the private collection of the author and will be deposited in the Geological Institute of the Greifswald University (no. GG 458/ 1-20).

Fig. 2 - Dendrina belemniticola, stenomorphically modified specimens from the Upper Campanian chalk of Mielnik (SEM-image of cast).

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Light microscopy of thin sections - physical configuration of fragile structures

Thin sections of Dendrina-infested belemnite rostra were used to assess the original topology of the hair-like extensions. This was necessary to exclude artifacts caused by water surface tension effects during the drying process of the casts. Most probably the original arrangement of the tiny hair-like extensions is modified.

The hair-like extensions are oriented perpendicularly to the rosette surface (Fig. 6). An exploration zone is formed around the rosette by the parallel arrangement of the hair-like extensions. The proximal parts of the extensions appear swollen and show a granular structure that corresponds to the bulbous swellings seen in the SEM-images (Figs 5d, f, 6). The distribution of these swellings determines the extent of the growth zone. Consequently, the Dendrina-rosettes are surrounded by two zones, a distal exploration zone and a proximal growth zone. The connection of the two zones as a functional unit explains the stenomorphism of D. belemniticola (Fig. 6).
DISCUSSION

The observed interaction patterns of the trace-making organism as well as the microendolithic structures described above help to explain how the endolithic trace-maker navigates in a non-homogeneous substrate, the boring process and the nature of the trace maker.

Fig. 4 - *Dendrina belemniticola* Mägdefrau, 1937 in belemnite rostra from the Upper Maastrichtian greensand of Nasiłów; casts showing the ontogenetic development of the trace. a) Two specimens of *D. belemniticola* preserved immediately after the penetration of the substrate. Note the entrance tunnels and apophyses (hair-like extensions) covering the young rosettes. b) Specimen of *D. belemniticola* preserved in an early developmental stage showing the symmetrical “butterfly-morphology”. Note the entrance tunnel and apophyses (hair-like extensions) covering the young rosettes. c) Specimen of *D. belemniticola* preserved in an early ontogenetic stage showing the symmetrical “butterfly-morphology”. Note that the apophyses (hair-like extensions) are not in a natural position but collapsed during the preparation. d) The same specimen as in c. e) *D. belemniticola*; cast showing a more mature ontogenetic stage of the rosette. Note that the apophyses (hair-like extensions) are covering the rosettes completely. f) *D. belemniticola*; cast showing a mature ontogenetic stage of the rosette. Note that the rosette is completely covered by the apophyses (hair-like extensions).
The exploration process - navigating in non-homogeneous substrates

The hair-like extensions (synonymous with the “apophyses” of Bromley & D’Alessandro, 1984, p. 236) can explain the stenomorphism of *D. belemnitica*. Such very fine structures are diagenetically sealed in most Upper Cretaceous carbonate deposits. Therefore neither light microscopy nor casting techniques are adequate to detect them (Schnick, 1999).

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Fig. 5 - *Dendrina belemnitica* Mägdefrau, 1937 in belemnite rostra from the Upper Maastrichtian greensand of Nasiłow; casts and thin sections showing the apophyses (hair-like extensions) of the trace. a) *D. belemnitica*; surface of the rosette (left) and proximal parts of the apophyses in thin section. b) *D. belemnitica*; surface of the rosette (background left) and proximal parts of the apophyses (SEM image of a cast). c) *D. belemnitica*; distal parts of the apophyses in contact with the substrate surface forming apertures (SEM image of a cast). d) *D. belemnitica*; surface of the rosette (left) and proximal parts of the apophyses showing a thickening caused by bulbous swellings (thin section image, compare SEM image f). e) *D. belemnitica* showing a hairy appearance caused by apophyses (hair-like extensions). Specimen from the Upper Maastrichtian greensand of Nasiłow (SEM-image of cast). f) *D. belemnitica*; proximal parts of the apophyses showing swellings that merge to a verrucose structure (SEM image). It is interpreted as the second stage of the boring process.
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The investigated belemnite rostra are internal skeletons that lack any protective structures or compartmentalization against endolithic infestation. Therefore, intact skeletons provide an extensive, homogeneous substrate suitable for the development of natural, uninhibited, fully formed growth-formed, idiomorphic endolithic traces (Bromley & D'Alessandro, 1984, p. 236). The general growth pattern of solitary D. belemniticola specimens is idiomorphic in belemnite rostra. Successive stages in its morphogenesis, from the initial penetration of the substrate to the mature endolithic rosette, are described above. Some of the Dendrina-ichnospecies introduced by Hofmann (1996) can be regarded as developmental stages in the ontogeny of one endolithic organism. Most probably they represent different growth phases of one and the same species, as shown for endolithic sponges by Bromley & D’Alessandro (1984, p. 232). There is only a slight stenomorphic adaptation to the outer convex belemnite surface compared to the ideal idiomorphic D. belemniticola.

Bioeroding organisms are dependent on a safe, i.e., robust and non-fragile endolithic environment. Consequently the trace maker of Dendrina avoided any direct contact with other borings. Its traces show a pronounced stenomorphism. Bromley & D’Alessandro (1984, p. 237) defined a stenomorphic boring as “a boring the form of which is affected by physical restriction in substrates such as thin mollusc shell or limestone that has been riddled previously by other endoliths”. This definition, originally introduced for sponge borings can be adopted for D. belemniticola. Voigt (1929, p. 122, taf. IV, fig. 10) described and figured two specimens that interfingered but did not amalgamate in the course of the boring process. This endolithic behavior is an essential feature of D. belemniticola. Consequently, a tangible wall of substrate remains between the borings to prevent fusion of the cavities.

Until now the question has remained unsolved as to how the trace maker of Dendrina could locate substrate limitations and interrupt the boring process as a precaution. Obviously there are certain similarities in the boring morphologies of D. belemniticola and Entobia isp. caused by the same practice of recolonizing an endolithic environment. Entobia isp. uses special sensory structures to explore the substrate. “Exploratory thread” is the name for “the most juvenile portion of sponge boring systems where linear growth predominates, consist of slender branching thread-like canals. Such threads are produced in order to locate the boundaries of the substrate and to investigate cavities within it” (Bromley & D’Alessandro, 1984, p. 236). They also introduced the term “apophysis” for “minute pin-prick or hair-like extensions that commonly extend from all parts of the sponge boring. In casts, these give the system a minutely spinose or hairy appearance” and characterized it as “probably a stunted form of exploratory process, and where the advancing

Fig. 6 - Dendrina belemniticola in thin section showing the void of the rosette (R) and the arrangement of the apophyses (hair-like extensions) in the surrounding substrate. Note that there is a growth zone (swollen apophyses of the proximal zone G) and an exploration zone (isodiametric apophyses of the distal zone E). Specimen from the Upper Maastrichtian greensand of Nasilow (thin section image).

Fig. 7 - Dendrina belemniticola - apertural canals probably created by fusion of closely spaced apophyses. a) A specimen from the Nasilow greensand. b) Specimen from the Mielnik chalk.
sponge approaches another sponge, the apophyses of each individual, in a network of exploratory threads, as if to map the progress of the competitor” (Bromley & D’Alessandro, 1984, p. 236). The latter describes exactly what is here found in the Nasiłów greensand specimens and explains the formation of stenomorphic Dendrina borings.

The boring process - controlled growth

Apophyses (hair-like extensions) have multiple functions. Their main function is exploratory but two subfunctions can be deduced resulting from this exploration: an expanding and a connecting function.

If there was enough appropriate substrate in the explored direction, the apophyses would be widened to enlarge the lumen of the rosette ideomorphically. This process would comprise both, centrifugally directed extension to enlarge the diameter of the rosette as well as laterally fusion of adjacent galleries that would produce the Dendrina-typical anastomosing pattern. In the latter case no preventing behavior would take place. The widening process would start with the radial growth of the apophyses to form bulbous swellings that constitute the typical verrucose surface of the Dendrina-rosette. Alternatively, swellings would grow directly out of the rosette to enlarge it. This growth process would be continued until the adult size of D. belemniticola was reached.

In contrast, if the substrate was not appropriate in the explored direction, the apophyses would form apertures at the substrate boundary and further penetration into the substrate would be stopped locally. The density of the apophyses is extraordinary high in the substrate space in-between the rosette-cavity and the adjacent outer substrate surface. Most probably, a change in function of the apophyses from exploring the substrate to connecting the endolithic organism with the exterior for respiration and nutrition would have occurred.

In addition, there is another, wider type of apophyses, i.e., apertural canals belonging to the endolithic system (Fig. 5b). It conforms to the definition of “apertural canal” introduced for sponges by Bromley & D’Alessandro (1984, p. 235): “the subcylindrical or slightly conical canal that connects the chambers or gallery with the aperture at the surface of the substrate”. Hofmann (1996, p. 66) described analogous structures for Dendrina-systems as “Verbindung zur Substratoberfläche” (meaning: “connection to the outer substrate surface of the substrate”). These apertural canals were most likely created by the fusion of closely spaced apophyses as described above (Fig. 7).

The nature of the trace-maker - a foraminifer without a test

Dendrina belemniticola is restricted to the Upper Cretaceous of northern Europe. It disappears at the K/Pg boundary. Comparable recent endolithic traces are not known. Therefore the taxonomic position of the trace-making organism remains uncertain. Traces of immured belemnite parasites as well as endolithic algae, foraminifers and sponges have been discussed (Quenstedt, 1849; Mägdefrau, 1937; Kutscher, 1972; Radwanski, 1972; Voigt, 1972). The parasite hypothesis can be ruled out as D. belemniticola has been found lying underneath broken surfaces of belemnite rostra (Kutscher, 1972). Radwanski (1972) proposed an algal trace maker. However, the absence of accompanying phototrophic benthic fossils in the offshore chalk facies indicates a palaeobathymetry well below the photic zone. Therefore the trace-maker was probably a heterotrophic organism and the hypothesis of an algal trace-maker has to be discarded (Hofmann, 1996). Bacterial and fungal producers are unlikely as well because of their small size. Additionally, traces of bryozoans differ distinctly in their general pattern and traces of macroborers can be excluded because of their size. Consequently endolithic sponges and foraminifers can be assumed as trace-making organisms.

Size, morphology and position within the substrate tier are distinct and predetermined in D. belemniticola. Compared to the boring of sponges there is less flexibility in using the substrate comprehensively. Sponges have a modular construction which gives them a greater plasticity in shape and size than is normally possible in unitary organisms. Furthermore, the sponge-typical camerate growth pattern is missing, and D. belemniticola does not show a branching of apophyses. In addition, there is no chip production as in the boring process of sponges. Instead Dendrina formation can be explained as a two-phase carbonate dissolution process. The sometimes pronounced cupulate micro-sculpture of D. belemniticola is very similar to that of the presumed sponge boring Entobia mikra Wisshak, 2008. Whereas in the latter case the detection of individual etching cells, occasionally “caught in action” (Wisshak, 2008), can be accepted as confirmation of a trace-making sponge, no such definite evidence was found for D. belemniticola so far. Further investigations should concentrate on the detection of this feature to evaluate the interpretation.

The probability of a foraminiferal origin of the dendrini ichnospecies Semidendrina pulchra Bromley, Wisshak, Glaub & Botquelen, 2007 was discussed by Bromley et al. (2007). Certain similarities in the rosette-shaped morphology compared to D. belemniticola can be detected in S. pulchra. However differences, such as ontogenetic development, rosette symmetry and general growth pattern as well as the shape, proportion and distribution of the hair-like extensions (Bromley et al., 2007; this paper) need to be considered. Nevertheless the fact that both traces are of foraminiferal origin and can be regarded as successive stages of adaptation cannot be excluded. Concerning adaptation of foraminifers to the endolithic habitat, a hypothetical line can be drawn from chasmoendolithic or cryptoendolithic nestlers with shells to increasingly complex naked euendoliths. The endolithic system D. belemniticola is probably a trace of an outstandingly complex and specialized organism.

In summary it can be stated that D. belemniticola most probably was created by a specialized endolithic foraminifer. The fossil record of endolithic traces attributed to foraminifers was summarized and discussed by Seuss et al. (2014). D. belemniticola may have been made by an originally test-bearing foraminifer adapted to the endolithic habitat as a so-called “naked foraminifer” in which a protective test was no longer needed. Apophyses and apertural canals of D. belemniticola made the exterior accessible for respiration and nutrition instead of the foramina of test-bearing foraminifers. The endolithic foraminifer was able to explore with its pseudopods both
the surrounding calcitic substrate as well as the outer marine environment.

ACKNOWLEDGEMENTS

This work is a contribution to the call for papers arising from the Fourth International Congress on Ichnology “Ichnia 2016 - Ichnology for the 21st century: (palaeo)biological traces towards sustainable development”, held in Idanha-a-Nova (Portugal), 6-9 May 2016.

I wish to express special thanks to Jörg Ansorge (Horst), Richard Bromley (København), Heiko Hüneke (Greifswald), Johannes Kalbe (Rostock), Dirk Knauß (Stavanger), Marcin Machalski (Warszawa), Klaus Vogel (Frankfurt am Main), Ireneusz Walaszczyk (Warszawa), Max Wisshak (Wilhelmshaven) and the members of the organizing committee of the “Ichnia 2016” for encouraging, inspiring discussions, logistic and technical support. The manuscript benefited from valuable referee comments.

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