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Remarks on the nature of belemnicolid borings *Dendrina*

ABSTRACT: The belemnicolid borings *Dendrina*, regarded previously as attributable to parasites of the belemnites, or to organisms benefiting from belemnite carrion, are interpreted as left by hard-substrate borers inhabiting loose guards lying on the sea bottom. The boring activity was herein confined to these parts of guards which projected above the bottom. With regard to taphonomical analysis, a conclusion arises that the boring activity may be presumably attributed to primitive algae.

INTRODUCTION

The rosette-shaped borings *Dendrina* that commonly occur on guards of the Upper Cretaceous belemnites have been the subject of scientific interest since F. A. Quenstedt's time. Nevertheless, the nature of these borings, both as regards their producers and mode of making is so far unknown and still remains enigmatic.

For many years, following Quenstedt's (1849, p. 470) suggestions, these rosette-like borings were regarded as formed during the belemnite life and taken into account as resulting from parasites activity in the belemnite body, supposedly on the surface of its guard (Voigt 1929, p. 122; Mägdefrau 1937; *cf.* also Pugaczewska 1965). An opinion has also been expressed, succeeding and modyfying Dacqué's (1921, p. 457) conclusions, that the boring organisms penetrated into the belemnite body after its death at the moment when the corps on the sea bottom were lying as carrion (Najdin 1969, p. 163). More recently, the advanced authors have regarded the discussed borings as belonging to a general category of the borings (Häntzschel 1962, Kennedy 1970). Concerning the nature of borings and their producers, all the above authors regard them as rather mysterious, although during the last years some suggestions on their possible relation to a zygotic resting stage of certain algae have been expressed, and analogies to a concrete Recent species, *Gomontia polyrhiza* (Lagerheim)[1], have been pointed out (Kornmann 1962; Boekschoten 1966, p. 346; Kennedy 1970, p. 274).

The discussed rosette-like borings are taxonomically included into the ichnogenus *Dendrina* Quenstedt, 1849, in the limits of which Mägdefrau (1937) established three ichnospecies, viz. *Dendrina belemniticola, D. anomala* and *D. incomposita.*

A majority of the investigated borings belong to the ichnospecies *Dendrina belemniticola* Mägdefrau, and single specimens (Figs 1*a*, 2*c*, 3*b*, and in greater number — Fig. 5) to *Dendrina anomala* Mägdefrau. The presented material (Figs 1—5) have been collected with guards mostly of *Belemnitella mucronata* (Schlotheim) occurring in the Chalk at the Campanian/Maastrichtian boundary (*cf.* Pożaryski 1960) of a glacial erratic mass ("floe") at Mielnik on the Bug river, Eastern Poland. In the Chalk of this erratic "floe" the guards of various belemnites have commonly been subjected to the activity of many boring and encrusting organisms, systematically described by Pugaczewska (1965)[2] who also recorded the presence of the discussed *Dendrina belemniticola* Mägdefrau.

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DISTRIBUTION OF *DENDRINA* ON THE GUARDS

The investigations of the *Dendrina* borings in the guards of *Belemnitella mucronata* (Schlotheim), the most common belemnite species at Mielnik, was justified in that the author wanted to recognize the distribution of these borings on the guards of the same belemnite species, in order to study their previously supposed parasitic origin. In these guards the *Dendrina* borings are the most frequent of the other, various belemnicolid borings, such as *Calcideletrix, Dictyoporus* and *Talpina,*

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[1] Various borings in shells and belemnite guards from the Lower Jurassic of Germany, attributed to this alga or its fossil relative by Pratje (1922), were actually made by a fungus (Bromley 1970, p. 55).

[2] Some determinations of these secondary settlers, given by Pugaczewska need a revision, as follows:

"*Calcideletrix flexuosa* Mägdefrau", presented in her Pl. 1, Fig. 3 really represents *Dendrina anomala* Mägdefrau (*cf.* Mägdefrau 1937, Pl. 4, Fig. 5; and Fig. 5 of this paper);

"*Pycnodonta* sp." presented in her Pl. 12, Fig. 1 really is *Gyropleura ciplyana* de Ryckholt (*cf.* Nestler 1965, Pl. 4, Fig. 5*b*);

"*Serpula (Dorsoserpula) lumbricalis* Schlotheim", presented in her Pl. 6, Fig. 3 and Pl. 7, Figs 2—4 is evidently another species, this former being really a Jurassic one.

the occurrence of which is so sporadical that any constructive discussion is hardly possible.

Practically everyone of the guards of *Belemnitella mucronata* (Schlotheim) at Mielnik are infected by *Dendrina* borings. The guards devoid of the discussed borings are exceptional. The majority of guards bear, however, single borings or very few only the distribution of which is not instructive. On about one-fourth of the guards the borings are more numerous and are then more conspicuously arranged in a patchy pattern, all the patches being distributed only in definite areas. These areas are variously oriented to the anatomical parts of the guards (Figs 1—3). Within the patches the borings are distributed in a more or less regular pattern, although there are places more densely populated (*e.g.* Fig. 2*c*, Fig. 3*d*). The boundary of the patches is usually distinctly sharp (*e.g.* Fig. 1. Fig. 2*c*, Fig. 3*c-d*), but in some guards single borings or a spot of a few borings sinuosize this line (*e.g.* Fig. 2*a-b*, Fig. 3*b*). Generally, the boring--infected patches longitudinally stretch along the guard and they usually cover an area smaller than one half of the guard.

The guards infected by the *Dendrina* borings over more or less the whole surface are rather rare, and it appears that these are usually more strongly infected on one side than on the other (Fig. 4).

INTERPRETATION OF BORING-INFECTED PATCHES

The presented mode of occurrence of the *Dendrina* borings and their arrangement in along-the-guard elongated patches allow to interpret such a distribution as a result of boring activity, of hitherto unknown producers, being confined to the parts of guards projecting from the bottom material. The boundary of patches corresponds to the contact line of the guards with the bottom sediment (*cf.* Fig. 1*a*, Figs 2—3 and Fig. 4*a*), and its local sinuosity (as pointed in Fig. 2*a-b* and Fig. 3*b*) — to uneven parts of the bottom, near to the contact with a guard. The bottom irregularities were of a primary nature or resulted from scouring action of bottom currents. It may be inferred that the guards were stabilely lying in a rather firm bottom material, and generally they have not been rolled over the bottom, as it is pointed by the *Dendrina*-infected patches strictly confined to a definite longitudinal sector of the guard. The patches appeared on the projected area which was haphazardly oriented to the anatomical parts: some patches come close to the apical (mucronal) part of the guard being buried mucro-upwardly (Fig. 3*a-b*), others — to the alveolar part of the mucro-downwardly buried guard (Fig. 3*c-d*, Fig. 4*d*), whereas the rest of patches is situated along the whole length of the flat or nearly-flat lying guards (Fig. 1*a*, Fig. 2*a-d*, Fig. 4*a*). The depth of burial varied, although as a rule the guards were buried in half of their volume or more. This certainly ensured the guards a stabile anchorage in the sea bottom (*cf.* Figs 2 and 3) and impeded their rolling by such hydrodynamic agents as currents, waving, etc.

It so happened that most of the guards were infected by *Dendrina* along their lateral or either latero-dorsal or latero-ventral sides (*cf.* mid-dorsal or mid-ventral lines marked on the guards in Figs 1—4). This relation seems to be rather accidental and resulting from a haphazard orientation of the guards on the sea bottom, as may be concluded from experiments by throwing the guards onto a flat surface, or rolling them over such a surface. As it appears, all these positions are not the most stabile or, at least, not the most preferential ones.

Examples of distribution of the *Dendrina*-infected patches over the whole surface of a guard correspond to an overturning of the guard, by a bottom current, after the first *Dendrina* activity, and stabile anchorage during the subsequent *Dendrina* activity (*cf.* Figs 4*a* and 4*d* — in this example successive *Dendrina* patches are distributed in areas contacting along one of the lateral sides of the guard).

TAPHONOMICAL REMARKS

The presented interpretation simply explains the distribution of *Dendrina*-infected patches on the guards here considered. In their mode of distribution these patches do not in any way differ from various borings confined to the skeletal parts projecting over the sea-bottom surface, as illustrated *e.g.* for clionid borings in *Belemnella lanceolata* guards by Najdin (1969, Text-fig. 49), boring algae in Miocene scaphopods (Boekschoten 1966, Plate I*A*)[3], various borings associated by epibionts in both Recent and fossil material (Boekschoten 1967)[3], and others.

Concerning the boring activity in loose belemnite guards lying on or in the sea bottom, it was Mägdefrau (1937, p. 64) who first recorded that some Upper Jurassic belemnites, *Hibolites hastatus* (Blainville) from Southern Germany, were bored[4] in various parts which had projected over the bottom. At present, the same opinion is expressed by Marcinowski (1972 — *cf.* his Text-fig. 2) for Upper Cenomanian *Actinocamax* gua-

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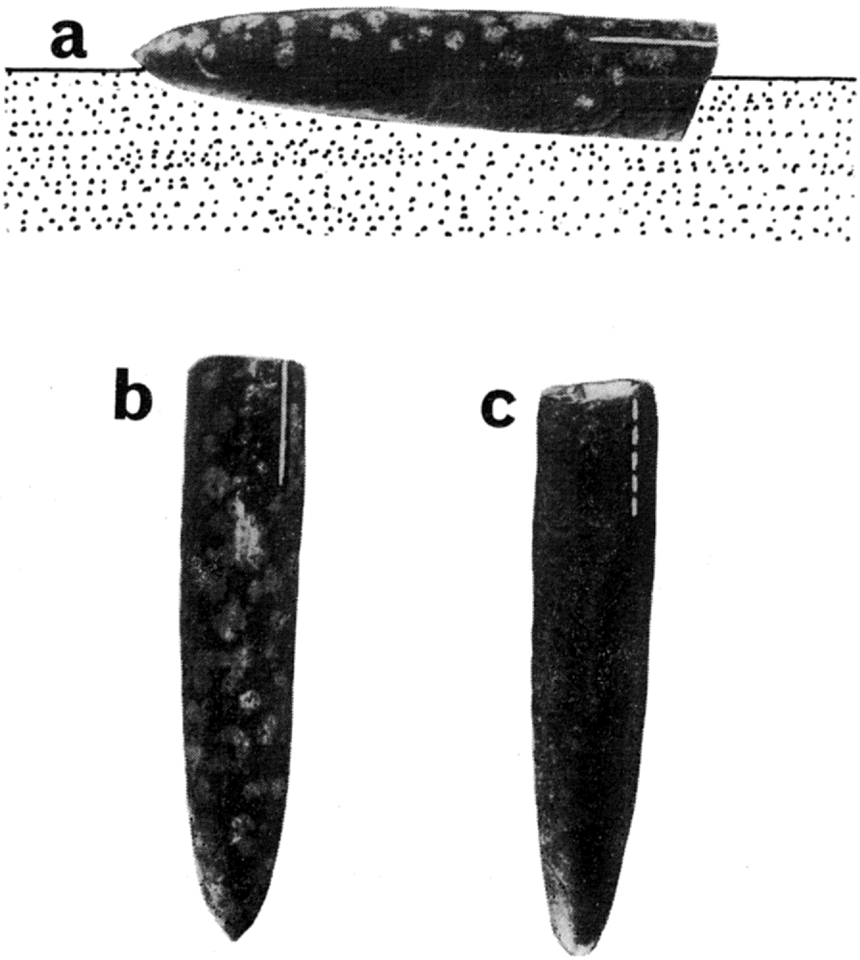
[3] The examples given by Boekschoten (1966, 1967) are referred to shells of alive, endo-benthic animals, more or less deeply buried in the sea bottom during their life.

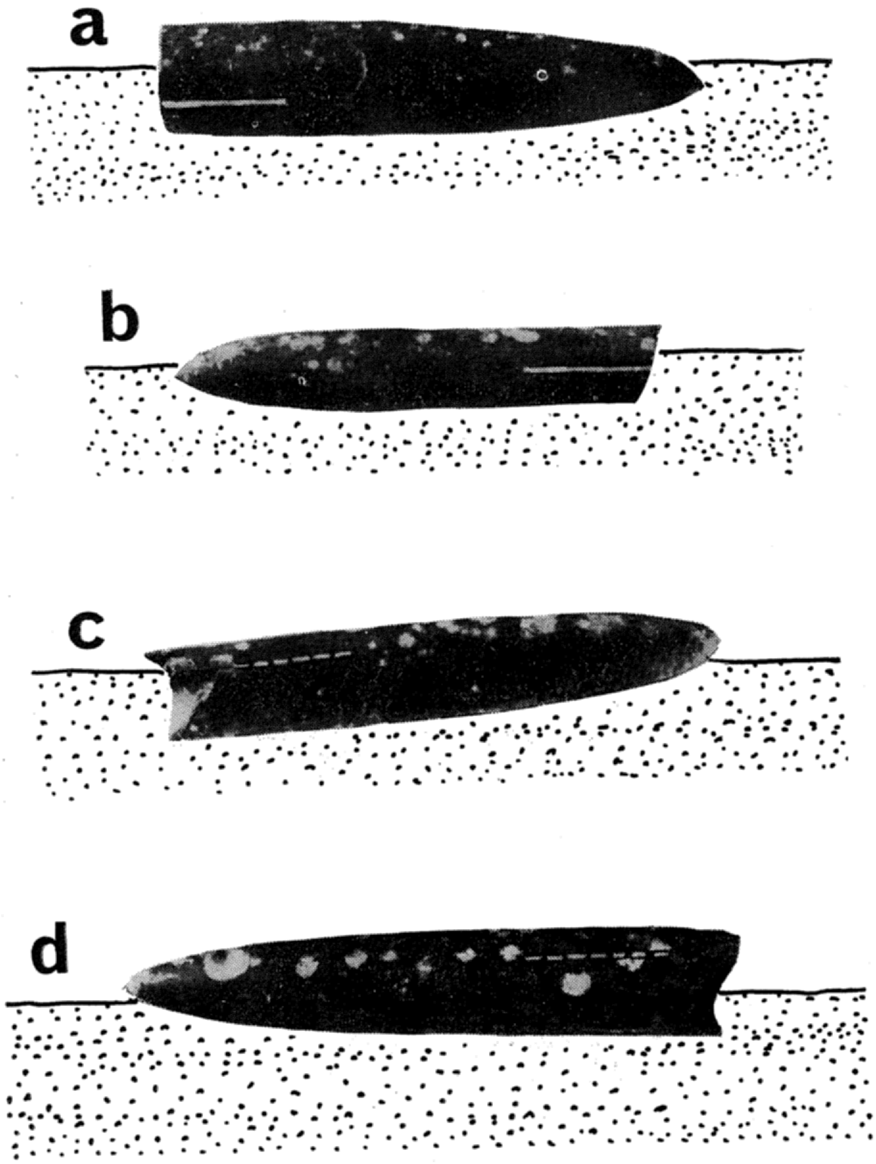
[4] These borings, assigned to the ichnogenus *Chaetophorites* Pratje, 1922, have previously been attributed to algae (Pratje 1922, Mägdefrau 1937), and recently to fungi (Bromley 1970 — *cf.* also footnote *no.* 1).



Distribution of a *Dendrina*-infected patch on the guard of *Belemnitella mucronata* (Schlotheim) from Mielnik; nat. size

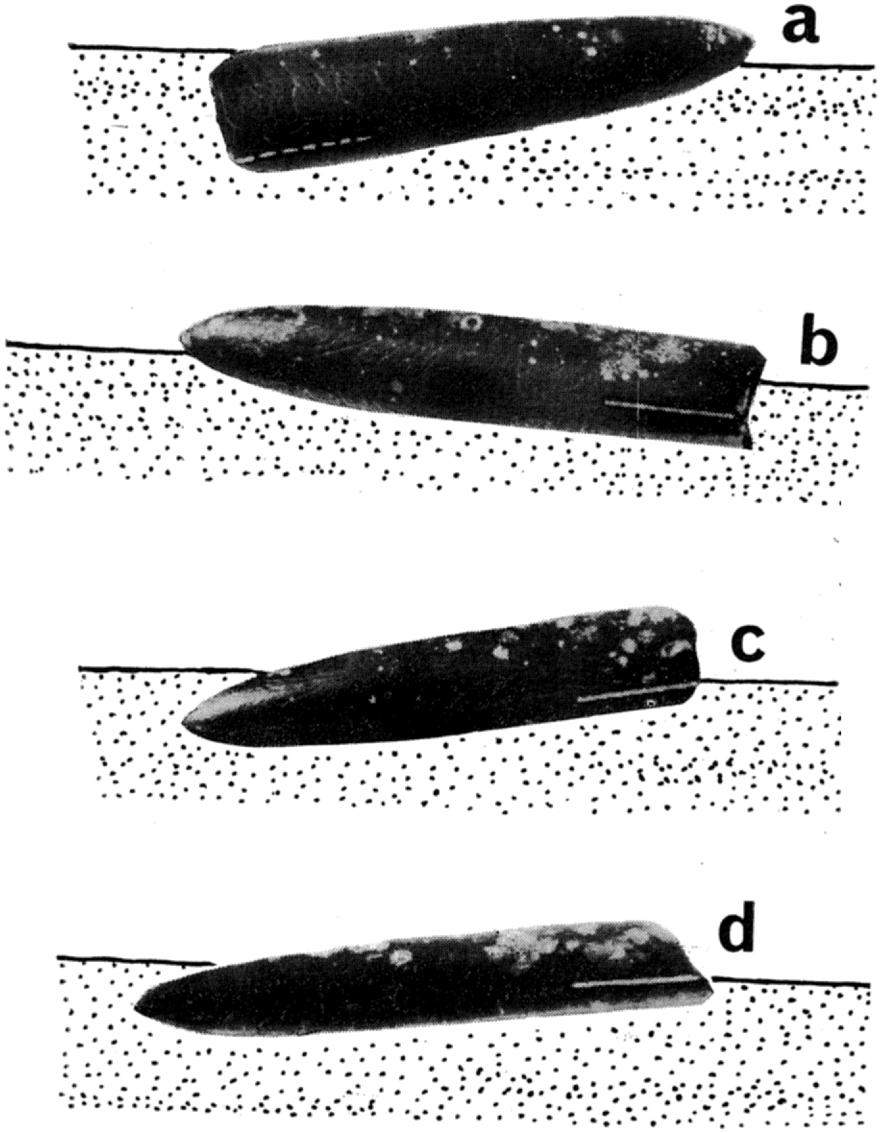
a side view of the guard in a supposed position, when partly buried in the sea bottom; *b* top view of the *Dendrina*-infected patch; *c* opposite side to that presented in *b*

Mid-dorsal and mid-ventral line are marked on the guard by full or broken line respectively



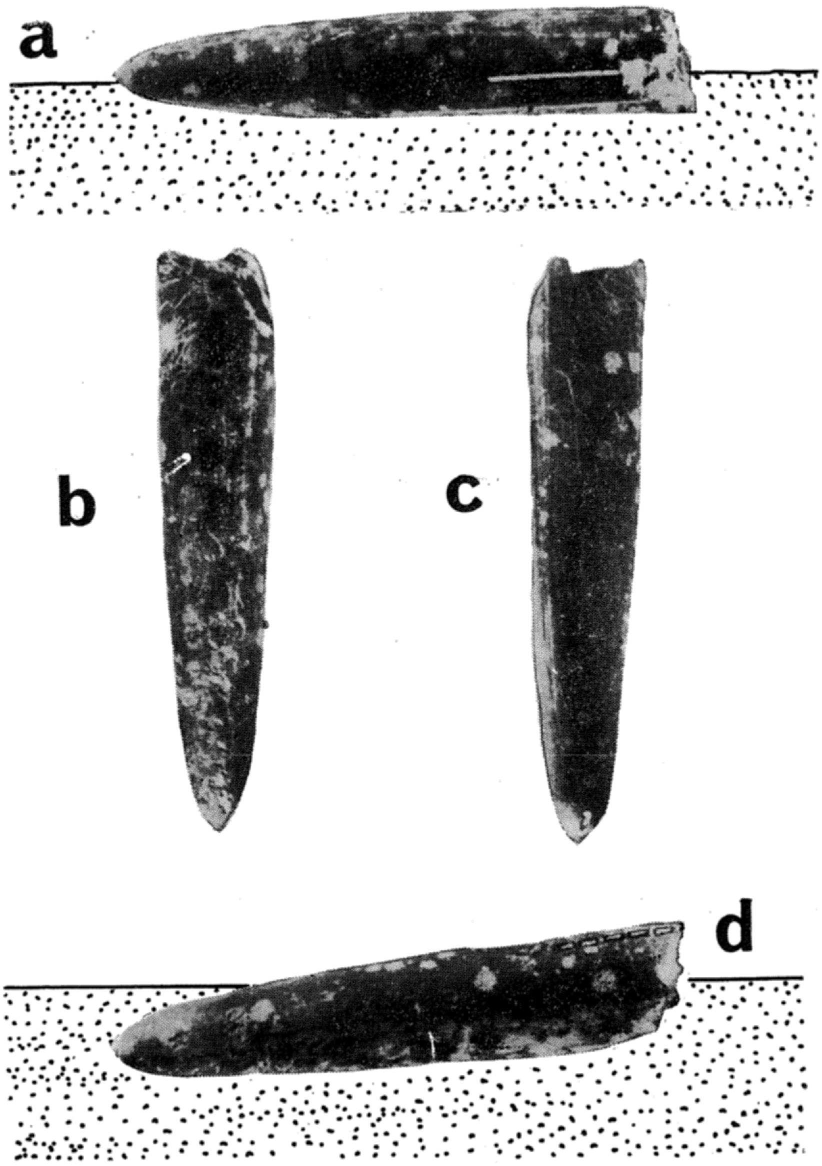
Dendrina-infected patches distributed along the guards of *Belemnitella mucronata* (Schlotheim) from Mielnik; nat. size

a—d various guards in a supposed, flat-lying position in the sea bottom (mid-dorsal or mid-ventral line is marked on the guards); the epizoic pelecypod *Dimyodon nilssoni* (v. Hagenow) is visible at mucronal part of the guard presented in *d;* detailed explanation in the text



Dendrina-infected patches distributed obliquely on the guards of *Belemnitella mucronata* (Schlotheim) from Mielnik; nat. size

a—d various guards in a supposed, oblique-to-the-bottom position (mid-dorsal or mid-ventral line is marked on the guards); detailed explanation in the text



Distribution of two different *Dendrina*-infected patches on the guard of *Belemnitella mucronata* (Schlotheim) from Mielnik; nat. size

a side view of the guard in the supposed first position on the sea bottom; *b* top view of the *Dendrina*-infected patch presented in preceding figure; *c* opposite side to that presented in *b* (marginal parts of both *Dendrina*-infected patches are visible); *d* side view of the same guard in the supposed second position, after a rolling over and a deeper, but oblique burying in the sea bottom (the second patch overlaps the first one along the lateral, facing-the-spectator side of the guard)

Mid-dorsal and mid-ventral line are marked the same as in Figs 1—3; detailed explanation in the text rds from Poland. A patchy distribution, resulting from the discussed position of the guard, was also recognized by Najdin (1969) who did not however present a definite conclusion.

The patchy distribution of the *Dendrina* borings may also be compared to various post-mortal borings situated along either a part or the whole surface of belemnite guards, as illustrated *e.g.* for clionids by Nestler (1960, Pl. 1, Fig. 2 = 1965, Pl. 7, Fig. 1) and Najdin (1969, Text-fig. 50 and Pl. 3, Fig. 1*a*-*b*), as well as for some acrothoracican barnacles by Codez & Saint-Seine (1957, Pl. 38, Figs 1—2) and Seilacher (1968, Fig. 1*a* and Fig. 2*c*-*d*) [5].

The presented conclusions although pointing to an irreality of interpretation of the *Dendrina* borings either as a result of life activity of parasites in the belemnite body — already previously questioned (Birkmann, *vide* Mägdefrau 1937, p. 63; Najdin 1969, p. 153) — or as a result of activity of organisms benefiting from the belemnite carrion, give no hints either on the nature of the boring-producers, or on the mode of formation of the borings just below the surface of the guards. In this matter only some following suggestions may be presented.

The *Dendrina*-occupied patches are as a rule devoid of other borings, which infect most of the guards in the Chalk at Mielnik. These patches are also devoid of various epizoans, the exceptions are very rare indeed (*cf.* Fig. 2*d* and Fig. 5) and consist in the presence of pelecypods *Dimyodon nilssoni* (v. Hagenow). The latter epizoic encrustations are obviously post-*Dendrina* in character (*cf.* Fig. 5). It may therefore be inferred that the *Dendrina*-occupied patches, during their inhabitation by the *Dendrina* producers, were covered by a film or a peel protecting the

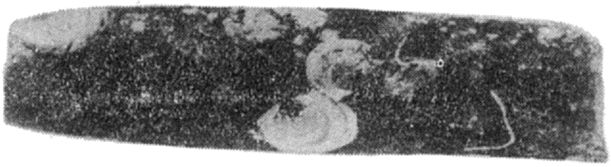


Fig. 5

Epizoic pelecypods *Dimyodon nilssoni* (v. Hagenow) encrusting the guard of *Belemnitella mucronata* (Schlotheim) successively after the *Dendrina* activity (*Dendrina belemniticola* Mägdefrau and *Dendrina anomala* Mägdefrau are visible underneath the destroyed valves of *Dimyodon*); besides, a few borings of supposedly tiny polychaetes are present; nat. size

The specimen collected at Mielnik by Prof. Dr. H. Makowski

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[5] Noteworthy are other acrothoracican borings in belemnite guards (*cf.* Saint-Seine 1954, Pl. 20, Figs 3—4; Seilacher 1968, Fig. 1*b*-*d* and Fig. 2*a*-*b*) which are evidently pre-mortal and result from a commensal relationship of acrothoracican barnacles and belemnite host, as it was suggestively explained by Seilacher (1968).

infected surface from the boring and encrusting activity of other organisms. It might have been a peel of primitive algae or seaweeds (similar *e.g.* to that presented by Boekschoten 1967, Fig. 1), which satisfactorily protected the substrate against the settling of other bionts. The encrusting epizoans settled on the *Dendrina* patches in the discussed environment at the moment when the algal peel had been destroyed and the belemnite guards had not yet been covered with sediment. The statement — resulting from the referenced bibliography and investigated material at Mielnik — that the *Dendrina* borings are practically confined only to the belemnite guards, may be explained by an adaptation of the *Dendrina*-producing bionts to the boring activity exclusively in this very substrate. Finally, the conclusion on the presence of an algal peel during the activity of the *Dendrina* producers leads to a suggestion that the *Dendrina* might have really been (*cf.* Kornmann 1962, Boekschoten 1966, Kennedy 1970) the borings of a zygotic resting stage of some algae, such as *Gomontia polyrhiza* (Lagerheim) in the Recent or its ecological equivalents in the past.

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UWAGI O NATURZE WYDRĄŻEŃ *DENDRINA* W ROSTRACH BELEMNITÓW

(Streszczenie)

Rozetkowate wydrążenia zaliczane do ichnorodzaju *Dendrina* Quenstedt, 1849, a często spotykane na rostrach górnokredowych belemnitów, interpretowane były dotychczas w zasadzie jako efekt działalności pasożytów w ciele belemnita (Quenstedt 1849, Voigt 1929, Mägdefrau 1937, Pugaczewska 1965) lub działalności organizmów trupożernych (Najdin 1969).

Materiał zebrany wśród rostrów *Belemnitella mucronata* (Schlotheim) z osadów senonu kry lodowcowej w Mielniku nad Bugiem upoważnia do wniosku, że działalność organizmów drążących musiała zachodzić na rostrach luźno już leżących na dnie morskim. Pola zajęte przez wydrążenia *Dendrina* — ichnogatunek *Dendrina belemniticola* Mägdefrau, 1937 — ograniczone są bowiem linią, która obrzeżała część rostrum wystającą z osadu (fig. 1—4). W oparciu o fakt, że działalność organizmów narastających (por. Pugaczewska 1965) wykluczała się w zasadzie z działalnością organizmów pozostawiających wydrążenia *Dendrina*, zaś w tych przypadkach, gdy następowała na tym samym rostrum, zachodziła później w stosunku do tej ostatniej (fig. 5), wyrażono pogląd, że w momencie wytwarzania wydrążeń *Dendrina* wystające z osadu rostra musiały być pokryte czymś, co uniemożliwiało osiedlenie się organizmów narastających. Był to najprawdopodobniej „kożuszek" sinic lub glonów, wśród których mogły znajdować się zarazem formy zdolne do działalności drążącej (podobnie jak niektóre formy dzisiejsze), prowadzącej do utworzenia rozważanych wydrążeń.

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